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BREEDING HABITS OF THE ORTHOPTERA.

CLARENCE L. TURNER.

CONTENTS.

INTRODUCTION.*

The Orthoptera are the most primitive insects according to Palæontological evidence. During the early Carboniferous period the insect. fauna was composed entirely of the ancestors of this group, and during the latter part of the period the members of this stock far outnumbered that of any other order of insects. Fossil evidence proves that many of the primitive types are represented at the present by species that, in spite of the long intervening periods, have changed but little. New types have arisen, however, until the Orthoptera as they are now classified vary widely in their structure and habits, some being adapted to living in trees, others for life upon bushes and grass, others for cave and burrowing life and still others becoming social parasites, living in the nests of ants and obtaining their food from their hosts. As adaptations for the various modes of life have taken place certain phases of behaviour have kept pace and now present as many aspects as the varied structures and habits of the insects themselves.

One of the most important of these special phases is that which attends the breeding activities and it is mainly with this aspect that this paper is concerned. It is impossible to describe the reproductive habits of all the Orthopteran forms as literature does not exist which would give the desired information. The activities of enough forms have been described, however, to permit a general comparison and a few generalities from the evidence thus presented.

The series of movements into which the entire process of reproduction may be divided will be considered separately and will be compared as units through the different families.

MOVEMENTS PRELIMINARY TO COPULATION. SEX DISCRIMINATION.

In some of the Orthoptera the movements preliminary to copulation are exceedingly simple. In others there is a complicated series of activities. Behaviour is the only criterion by which we may judge sex discrimination. It has been suggested that any movement which would indicate excitement after the two animals have come within sensing distance of each other might indicate recognition of sex. It must be borne in mind, however, that some of the Orthoptera are in a state of continual excitement during the breeding season, especially is this the case with males which have once copulated. In this state of excitement males will seize other males, members of other species or even a stick to which the abdomen of a female has been attached, so that it is not safe to base sex discrimination upon this one peculiarity of behaviour. On the other hand there is an entire lack of movements that would indicate excitement in some forms. Here the problem of sex discrimination is just as puzzling. No general statement in regard to sex discrimination would hold and each case must be considered separately.

The records of the sexual activities of the Blattidæ are very meager and in no case have their habits been described in detail. The sense of hearing is obviously not a factor as there are no organs for the reception of sound. Sight plays some part, for the male is described as running about the female trailing his abdomen and attempting to induce her to become quiet, even before they have come into contact with their antennæ. The senses of touch and of odor must play some part although no statement can be made as to their relative importance.

The Mantids have a very simple courting. When a male is introduced into a cage with a female during the breeding season he approaches her, raises his thorax, lowers his head and stands in this fixed position for some time. The female apparently pays no attention to him during this performance. After introducing himself in this manner he simply mounts the back of the female and copulation takes place. All the movements which are characteristic of the courting attitude occur before any contact of the antennæ or bodies has been established, so that touch and contact-odor seem to be secondary. There are no records of one male attempting to seize another, otherwise it might be contended that the sense of sight merely guided the two animals together and that the actual discrimination depended upon contact. Since discrimination is accomplished before any contact has been established, it seems that the most important factor is sight.

The Phasmids of which the walking sticks are common representatives, have very simple preliminary movements. They are mostly nocturnal in their habits and copulation takes place at night or in very dim light. No contact seems to be necessary and if sight furnishes the male with any information concerning the sex of his mate there is no excitement to indicate the fact. Without any preliminary movements whatever, the male mounts and copulates. Stockard ('08) describes some interesting experiments in which he proves that no complex combination of the senses are required for accomplishing sex discrimination. He cut off the end of the female's abdomen and fixed it to a stick which had been furnished with wire legs and it was found that the male copulated with this piece of abdomen quite as readily as with the normal female. Stockard also maintains that the experiment proves that no response on the part of the female is necessary to induce the male to copulate.

The Acrididæ or short-horned grasshoppers include a great number of genera and species which show a wide variation in their structure and a lesser degree of variation in their behaviour. A more or less constant type of behaviour preliminary to copulation, however, makes it appear that sex discrimination is accomplished in the same manner for the entire group. One factor in the ordinary behaviour of the Acrididæ which may be of some significance for mating seems to have been entirely disregarded. Most of the insects have organs for the reception

of sound. During flight a dry crackling sound is made by the wings and there is a brilliant display of color. It seems reasonable that organs for making and receiving sounds which play so important part in the sexual activities of the Locustidæ and of the Gryllidæ should not be without a similar function here. The usual movements of the male of the Acrididæ consist of a few convulsive jerks of the body as he sights the female, followed by a creeping toward her until he is within springing distance. Some investigators have stated that the male will spring upon the female from a distance of three or four feet. In the Tettigidæ (grouse locusts) this process is modified somewhat. The male does not spring but, creeping toward the female, he makes a rush and mounts from the side. It is not uncommon for males of one species to spring upon other males or for males to mate with the females of an entirely different species. Species differing as widely as Hippiscus rugosum and Melanoplus femur-rubrum have been found in copulation. These facts suggest that sex discrimination and even species discrimination is of a low order in this group. Sight and possibly sound furnish the stimulus for the beginning of the preliminary movements, but an actual body contact seems to be necessary for a final discrimination of sex.

The Locustidæ with their great variety of habits and structure furnish some of the most interesting variations in their preliminary movements. Some are nocturnal; some are diurnal; some are winged; some are not; some have very complex movements attending their copulation, some mate very simply. Some forms like the katy-did have membraneous organs in the wings for producing sounds. The shrilling of the male as he attempts to call the female to him is one of the most common sounds of the late summer nights. When a female has been induced to approach the male stops shrilling and the two indulge in a preliminary fencing with the antennæ. Here we may assume that the sense of hearing was the first factor used in bringing the two sexes together. The sense of sight evidently does not play an important part here. In the Mormon Cricket (Anabrus simplex), however, sight is apparently the most important factor while hearing plays a secondary part. Anabrus is diurnal and congregates in great numbers on the prairie during the breeding season. The preliminary movements have not been observed but since the only sound uttered is a faint

squeak, hearing does not seem to be so important. Among the Locustidæ are found species which are not only wingless but have no means of making sounds. These are nocturnal and representative. Ceuthophilus stygius, a species living in the caves of Indiana, has eyes that have become somewhat rudimentary. Since it breeds "far back beyond the reach of any rays of light," (Blatchley, '02) and is devoid of hearing organs, the only senses left to it for its sexual activities are those of smell and touch. In Ceuthophilus latens the writer found that although the eyes are well developed they are not used in the sexual activities of the animal, sex discrimination depending upon contact and possibly odor. In the Locustidæ then, sex discrimination is accomplished in some cases by contact (perhaps "contact odor") alone, in others by contact and sight and in still others by contact, sight and hearing.

The true crickets, or Gryllidæ, present nearly as wide a variation in their preliminary movements as do the Locustidæ. Chirping is a common habit with both the nocturnal and the diurnal crickets and is without doubt a sex call. In some of the nocturnal forms the sense of sight is evidently used but little and the sense of hearing is relatively important. The field and ground crickets have similar copulating habits. After a female has approached in response to the call of the male the usual fencing with the antennæ ensues and then the male, turning around and raising his wings, invites the female to mount. The tree cricket (Oecanthus) has been much observed and its habits described in detail. The female becomes greatly excited upon hearing the call of the male and in going to him in response to the call seems to be directed by the sound. (Jensen, 1908.)

The mole cricket (subfamily Gryllotalpinæ) breeds underground in tunnels which it constructs. (Baumgartner, '10.) Although it is obliged to carry on all its mating activities in the dark, the loss of opportunity to use the sense of sight is compensated for by the presence of a chirping organ in the female. She answers the call of the male until they have come into contact, and the problem of their uniting is simplified.

Sex recognition in the Gryllidæ is accomplished in all cases with the aid of the sense of hearing and in some without the possibility of aid by sight. How much of a part actual contact plays it is difficult to say, but the movements that would indicate a sexual excitement frequently are begun with the aid

of no other sense than that of hearing. In all the families previously mentioned, except the Locustidæ, the female is a passive party in the process of copulation. In the Locustidæ she plays an active part in coming to the male in answer to his call. In the Gryllidæ she must take a still more active part and actually mount the back of the male before copulation can take place. It is a far cry from the Phasmid in which the female is so passive that the male will copulate with her abdomen which has been fastened to a stick and the female of the cricket which must not only find the male but even mount his back. Little power of discrimination would be conceded to the female of the Phasmid while in the cricket it appears that the female must have a highly developed discrimination. Since in the Phasmid it would be simply lost motion for the male to go through a series of complicated movements before such an unresponsive female, no such movements have been developed and copulation is very simple. In the cricket, on the other hand, the male must first make his whereabouts known and must then demonstrate his sex before the female will mount. Sex discrimination in the female and complication of preliminary movements have developed hand in hand.

COPULATION.

Under this topic will be discussed mainly the relative position of the bodies of male and female during copulation, the duration of copulation and the method of transfer of spermatozoa.

Since in the Cockroach the process is so rapid that the details cannot be followed, it can only be said that the male shoves his body under that of the female and accomplishes the transfer of spermatozoa in a few seconds.

The male Mantid simply mounts and copulates sometimes retaining his position for as long as seven hours. The spermatozoa are transferred directly to the oviducts and if there is any spermatophore present it is not visible externally. The habit of cannibalism is highly developed among the Mantids. If a pair is kept in captivity during their copulation, the female will invariably devour the male, although he is usually given a respite of an hour or so. Not infrequently, however, the male is devoured during the actual process of copulation. This has been observed in nature as well as in animals kept in captivity. Fabre thinks that this habit is a relic of the Carboniferous

period when the Mantid was one of the few insects and when
there would be a natural dearth of food. Then the male was
habitually devoured as the most available source of food. A
female will copulate with as many as seven males in a single
season.

Copulation is as simple in the Phasmids as it is in the
Mantids. The male mounts the back of the female and curling
his abdomen under and to one side of that of the female he
effects the union. Copulation lasts for several hours.

The method of copulation in the Acrididæ is fairly constant.
The male, after assuming his position upon the back of the
female, bends his abdomen to one side and under that of the
female and copulates. Copulation between a single pair lasts
for hours and sometimes as long as two days. There is no
spermatophore, the spermatozoa being transferred directly to
the oviducts by a bifurcated intromittent organ.

In spite of the great variety exhibited in the structure and
habits of the Locustidæ there is a fairly constant mode of
copulation. It may be termed an "end to end" position. In
some cases both of the animals are in a vertical position on
grass stems; sometimes the male is curled beneath the female,
or even standing on his head. In the case of Ceuthophilus both
animals stand upright, facing in opposite directions, while the
end of the abdomen of the male is inverted and grasps that
of the female by the subgenital plate. This may be taken as a
typical position while the others are variations necessitated by
circumstances. The mating pair may be located upon parallel
or upon diverging stems, upon the ground in a horizontal posi-
tion or the female may be running about dragging the male in
any position. Copulation is of short duration, generally lasting
a few minutes and the spermatozoa are transferred by means of
spermatophore. This spermatophore when visible externally
appears as a lobed membranous sac which is translucent at first
but becomes opaque after a short exposure to the air. It
appears shortly after the union of the two animals and is
quickly transferred by the male to the vulva of the female
where it hangs until the contained spermatozoa have made
their way into the oviducts.

The relative position of the bodies of the male and the
female is constant throughout the entire group of the Gryllidæ.

The female mounts the back of the male and a spermatophore is fixed to her vulva by the male. The transfer of the spermatophore takes only a few minutes but the animals remain in their positions for a short time before separating. As soon as she is free from the male the female begins to gnaw at the spermatophore and it seems that nature has provided a special organ for keeping her attention diverted long enough to allow the spermatozoa to enter the oviducts. At the base of the male's wing is located a gland which exudes a viscous liquid which is evidently very palatable to the female for she gnaws at it constantly during copulation, and is kept occupied for some time after the spermatophore has been transferred.

From the evidence drawn it is safe to say that each family of the Orthoptera has a fairly constant mode of copulation, and that insofar as any specialization is shown it has its greatest development in the Locustidæ and in the Gryllidæ.

OVIPOSITION.

The process of egg-laying is very simple in some of the Orthoptera and complex in others.

The oviposition of the Cockroach may be considered a very specialized type. Sixteen eggs are deposited by the female in a horny capsule which is secreted inside of her body. Some of the Cockroaches deposit this capsule as soon as it is formed, while others carry it about, partially protruding from the body, until the young are nearly ready to hatch. Then it is deposited in some convenient crevice. The capsule is a brown, horny structure which is in the shape of a flattened oval measuring about 12 mm. in length and 6 mm. in width. It is furrowed by a series of fine annulations, and provided with a lateral notched carina. The eggs are arranged in two symmetrical rows of eight each.

Egg-laying among the Mantids is a very complicated process. A single female lays a great many eggs, all of which are deposited at one time and enclosed in a fibrous öotheca. The öotheca is attached to a twig, a stone, or to any suitable object that may be at hand. In making the ootheca a small amount of a viscous liquid is extruded from the oviducts and the genital plates immediately begin whipping the liquid into a foam. More liquid is extruded and the whipping continues.

From time to time the abdomen is buried deep in the mass, and it is supposed that actual egg-laying occurs at this time. The time required for completion of the egg case is about two hours. The öotheca as it is finally left by the female is a rough, oval structure composed in its interior of horny material which gives place near the surface to an alveolar structure. The outer covering resembles tough silk in its consistency. The eggs are arranged in regular tiers in the center of the case. The entire structure is an admirable one for resisting the rigors of the weather as well as the attacks of insects and of parasites.

The Phasmids have a type of egg-laying that appears to be most simple. The eggs are simply discharged at random and fall to the ground. The fact that a fairly well developed ovipositor still persists in the Phasmids which practice this random method of oviposition seems to indicate that this method of deposit is a recently acquired one.

When the female of the Acrididæ is ready to lay her eggs, she brings forward the end of her abdomen, and inserting it into the ground at a sharp angle to the axis of the body, she works the valves of the ovipositor and shoves with the abdomen until the entire posterior end of the body is buried in the ground. Having accomplished this, she fills the cavity which she has made with eggs arranged in oblique columns and at the same time she exudes a viscous liquid which fills the hole and binds the eggs together. Some of the grouse locusts on account of their small bodies and short abdomens can construct only shallow burrows. Such animals frequently lay in moss where the eggs are protected by their resemblance to seeds found there.

The Locustidæ and the Gryllidæ present a wide variation in their manner of egg-depositing. The Katydids live mainly on bushes and trees and deposit their eggs there. In some instances the eggs are glued to the side of a twig and in others they are stuck to the edge of a leaf, or even enclosed in the end of a leaf which has been split for this purpose. When a female is ready to deposit her eggs, she roughens the surface of the twig and removes any buds or other projections. Then bringing forward the end of her scimiter-shaped ovipositor she guides it into the correct position by means of her palpi and jaws and then emits a glue-like liquid which adheres to the twig. The egg then appears shiny black at first, but turns gray later and is glued fast so that it lies at a slight angle to the twig.

The process is repeated, each egg overlapping the preceding one, until a row has been deposited. The eggs are oval but are very much flattened, resembling hemp seeds in shape. The cone-headed grasshoppers have blade-like ovipositors of different shapes, some being short and curved, others very long, straight and pointed. These serve for inserting the eggs between the leaves and stems of grass upon which the insects live. Ground dwelling Locustidæ such as Anabrus and Ceuthophilus, have their ovipositors modified for piercing the ground. That of Ceuthophilus is slender but strong and is equipped with five teeth at its apex.

The ground and field crickets lay their eggs, singly or in groups of from two to five, in the ground. The long needle-like ovipositor is admirably adapted for thrusting into the ground. The tree crickets (Oecanthinæ) have retained the long, needle-like ovipositor but have modified its use to suit their changed habitat. Stems containing pith are usually selected for egg receptors, raspberry stems being most favorable. The female begins operations by biting the twig and roughening it so that the ovipositor may gain an entrance. The ovipositor is then brought up, placed upon the roughened spot and by vigorous working of the blades and thrusting with the abdomen, the twig is pierced to the depth desired. The egg is deposited and crowded tightly into the hole by the ovipositor after which it is covered and left. The same process is repeated until the twig contains a long row of eggs in the pith almost perpendicular to the long axis of the twig.

The mole crickets do not have a well developed ovipositor. The eggs are deposited by simply dumping them in a heap in one of the subterranean chambers. Contrary to the habits of the other crickets, however, the eggs are watched and cared for until they hatch.

On the whole the Acrididæ may be considered to have the most generalized type of egg-laying. The Blattidæ and the Mantids have been specialized in the direction of highly developed egg-cases while the Locustidæ and the Gryllidæ have become specialized in the habit of laying the eggs singly or in small groups, each single egg or group in its own prepared cavity.

SPECIALIZED AND SIMPLE TYPES OF REPRODUCTIVE BEHAVIOUR.

In considering the different aspects of the reproductive behaviour, (preliminary movements, oviposition, etc.), the Acrididæ appear to be the least specialized. The Cockroaches and the Mantids are specialized in the habit of constructing egg capsules and cocoons. The Locustidæ and the Gryllidæ have developed their preliminary movements to a great extent and also have a specialized type of oviposition, but different from the Cockroaches and the Mantids. The Acrididæ seem to be specialized in neither regard and occupy a somewhat intermediate position as regards egg-laying and preliminary movements.

BLATTIDAE   —32
             —23
MANTIDAE   —17
             —13
PHASMIDAE   —11
             —4
ACRIDIDAE   524
             ························148
LOCUSTIDAE   194
             ························214   NUMBER OF SUB FAMILIES
GRYLLIDAE   —64   ——— AMERICAN
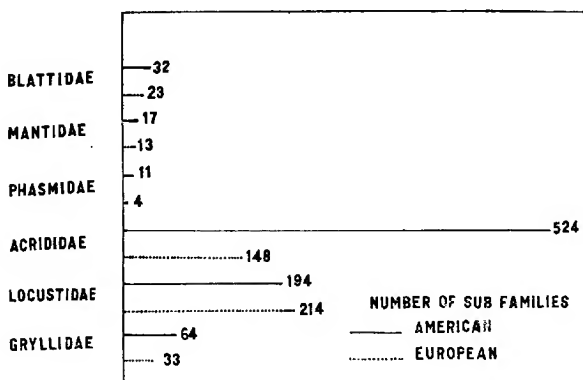   ····· 33   ············ EUROPEAN

FIG. 1. Diagram to illustrate effect of specialization upon the number of sub-families in each group of the Orthoptera.

It is a well known fact that specialization in any habit, especially in breeding habits confines the animal to a more limited field and lessens its chances for adjusting itself to changes in environment. Consequently the animal which has the more general habits can occupy the larger general field and so have a larger representation. Figure 1 represents the total number of subfamilies in each group of the Orthoptera in the Holoarctic realm. The Acrididæ far outnumber the other groups. Locally one subfamily may predominate as it finds conditions favorable to its mode of specialization; but ·in general, non-specialized conditions will prevail, and it is the type of animal which has the least degree of specialization that

will have the largest representation. It is possible that conditions have arisen in Europe that have been temporarily very favorable to the type of specialization of the Locustidæ, causing them to attain to greater diversity than the Acrididæ in that region or the Locustidæ in America.

The Phasmids and the Mantids have their greatest development in the tropics. Consequently they are poorly represented in the more generalized temperate climates of Europe and of the United States.

AN ATTEMPT TO CLASSIFY THE ORTHOPTERA ACCORDING TO THEIR REPRODUCTIVE BEHAVIOUR.

Figures 2, 3 and 4 are schemes based upon one or two factors of reproduction while Figure 5 represents a classification based upon all the factors collectively.
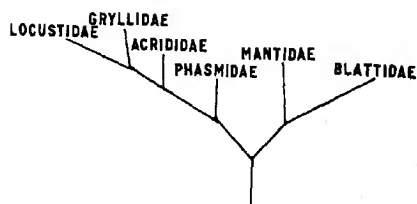
*Fig. 2. Classification based upon specialization of the ovipositor, Rudimentary ovipositor in Blattidæ and Mantidæ, intermediate development in Phasmidæ and Acrididæ, maximum development in Gryllidæ and Locustidæ.

In Figure 2 the classification is based upon the amount and direction of specialization of the ovipositor. The first division separates the Mantids and the Cockroaches from the others because of the lack of an external ovipositor. In both forms the ovipositor is relatively undeveloped. The Phasmids are included with the Acrididæ, the Gryllidæ and the Locustidæ because they have a fairly well developed ovipositor although it apparently is not used. The Acrididæ are separated from the Locustidæ and the Gryllidæ because of their relatively short and undeveloped ovipositor. The Locustidæ and the Gryllidæ as a whole have highly specialized ovipositors although some have suffered an almost complete loss of the organ due to their change of life. Reading from right to left we have a more or

*In Figs. 2, 3, 4 and 5 direction and extremes of factors used in classification are indicated in horizontal plane.

less regular sequence; first, the non-development of an external ovipositor; second, an ovipositor developed but nonfunctional; third, a comparatively unspecialized ovipositor and lastly, a highly specialized and functional ovipositor.

The classification in Figure 3 is based upon the presence of a definite egg-capsule or the approach to it in those forms which do not possess it. As in Figure 2 the Mantids and Blattids stand apart from the other forms being divided from the other forms because of their possession of an egg capsule or öotheca. The Locustidæ and the Gryllidæ again occur at the other extreme, because they lay their eggs singly or in masses of only two or three. Again the Acrididæ occupy an intermediate position because they resemble the Blattidæ and the Mantidæ in
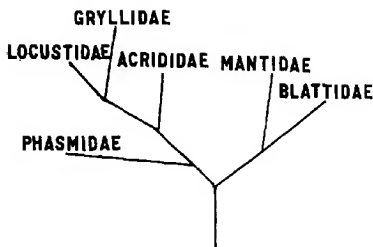

Fig. 3. Classification based upon the occurrence of an egg capsule. Mantidæ and Blattidæ having a definite ootheca are placed by themselves. Gryllidæ and Locustidæ laying eggs singly are placed at the opposite extreme. Acrididæ, laying eggs in compact mass are placed between. Phasmidæ are placed near Acrididæ because eggs are all discharged at once. Since they have no approach to an ootheca they are inclined to the left extreme.

laying their eggs all at once but in not having a definite egg capsule. The position of the Phasmids in this classification is doubtful. The fact that they choose no special place for depositing their eggs and that they deposit them in a very loose manner, indicates a rather low degree of specialization. They have been placed near the Locustidæ and the Gryllidæ because they resemble these families in depositing their eggs singly.

In Figure 4 three factors are considered in the classification of one of the stems established in Figures 2 and 3. These factors are the presence or the absence of a spermatophore, the relative position of the bodies during copulation and the duration of copulation. The three factors are intimately associated.

Long duration of copulation, the absence of a spermatophore
and the superposition of the body of the male during copulation
divides the Phasmids and the Acrididæ at once from the
Locustidæ and the Gryllidæ. Minor peculiarities in these
factors permit a division between the Acrididæ and the Phasmids.
The Locustidæ and the Gryllidæ have a short duration of cop-
ulation, and a spermatophore which is usually visible. The
Locustidæ and the Gryllidæ may be divided upon the ground
that there is a superposition of the body of the female in the
Gryllidæ and an "end to end" position of the bodies in the
Locustidæ. The mole crickets may be divided from the other
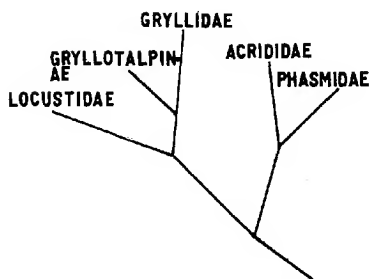Gryllidæ because of their peculiar modification of the usual
body position.

Fig. 4. Classification based upon the development of spermatophores in
those forms showing an inclination toward this structure. Acrididæ and Phas-
midæ, having sperm masses resembling spermatophores but not enclosed in a
membrane, are placed at one extreme. Gryllidæ have definite spermatophore,
but highest development is reached in Locustidæ, which are placed on the left
extreme.

An attempt is made in Figure 5 to summarize the factors
that have been named as well as some additional ones. The
main division is made because of the following facts: The
Blattidæ and the Mantidæ have a definite egg capsule or
ootheca; they have no development of an external ovipositor for
inserting eggs into the ground or into twigs and they neither
produce sounds nor have organs for the reception of sounds.
The other groups are united because they possess ovipositors,
because they have organs for producing and receiving sound
and because they do not lay their eggs in a capsule. The posi-
tion of the Phasmids is doubtful but a consideration of all their
breeding habits will place them in the position shown, nearer to

the Acrididæ than to the Mantidæ. The Blattidæ and the Mantidæ may be divided because of the peculiar manner in which each constructs its egg case. A further subdivision of the Blattidæ is made to include the myrmecophilous forms. The stem including the Acrididæ and the Phasmidæ is separated off because of the following factors: These two forms have a relatively poor development of the ovipositor, and a superposition of the body of the male during copulation. Eggs are laid all at one time, sounds are produced which consist of a crackling of the wings, hearing organs are present and are located in the base of the abdomen. In the Locustidæ and the Crickets on the other
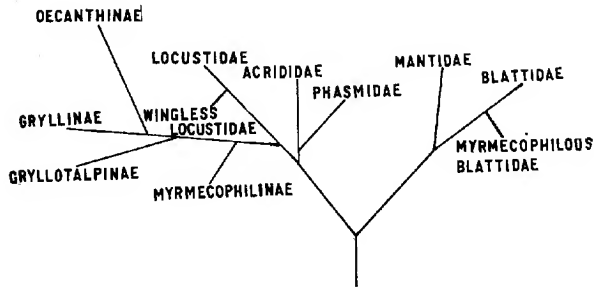
*Fig. 5. Classification based upon summary of factors in three preceding schemes. Right extreme indicates presence of definite ootheca, long duration of copulation, superposition of body of male during copulation (in Mantidæ), absence of organs for production and reception of sounds and the absence of an ovipositor. The left extreme indicates a complication of movements prior to copulation, absence of an ootheca, eggs laid singly, superposition of body of female during copulation, presence of stridulating organs and organs for the reception of sound. Forms placed in various intermediate positions show a lesser degree of specialization.

hand the ovipositor is well developed and specialized, the bodies are found in various positions during the copulation but there is no superposition of the body of the male, eggs are laid singly or in masses of two or three, sounds produced consist of chirps, and the organs for the reception of sounds are located in the anterior tibia. The Acrididæ and the Phasmids are separable because of differences already mentioned. A subdivision of the Locustidæ is made because some forms have suffered a degen-

*Horizontal plane indicates general direction and extremes of summary of factors and processes used in classification. Lines inclined upward indicate development and specialization of organs and processes, while lines inclined downward indicate degeneration or loss of organs. Extent of lines indicates to some degree the amount of development or degeneration.

eration of those very factors which mark them off from the
other groups. The forms that have entirely lost their wings
have lost their capacity for producing sounds. In Ceuthophilus
the organs for the reception of sound have also been lost. The
factors by which we may divide the Locustidæ from the Crickets
are not so conspicuous. The modification which the ovi-
positor has undergone in each group will suffice for their
division. The relative position of the bodies of the male and of
the female during copulation is another factor which may divide
them. The diversity found among the crickets makes further
subdivision possible in that group. The activities of the field
crickets may be regarded as the most typical for the Gryllidæ.
The tree crickets (Oecanthinæ) being specialized in their manner
of ovipositing are given a separate standing. The mole crickets,
because of the absence of the ovipositor, the changed manner of
depositing the eggs, and because of the development of a
chirping·organ in the female, have been placed in a separate
division. Little is known of the reproductive habits of the
myrmecophilous crickets and Blattids. In European forms
only the females have been discovered. Both males and
females, however, have been found in an American form by
Wheeler. (Wheeler, 1900.) The reproductive activity must
differ somewhat from the typical mode. Consequently they
are given a separate rating as indicated in the diagram.

Having made such a classification it must be admitted that
the behaviour of each group depends to some extent upon
structural characteristics so that the classification really rests
upon morphological characters, the basis adopted by tax-
onomists for classification. The structural characteristics
have been used, however, only when they have some intimate
connection with the reproductive behaviour.

A glance at the ancestral tree of the Orthoptera, (Fig. 6), will
show some striking resemblances to the classification based
upon the reproductive behaviour (Fig. 5). The fossil evidence
bearing upon the ancestry of the Orthoptera has been thor-
oughly worked out by Anton Handlirsch ('08), and a genealog-
ical tree constructed to show the relations of the different fam-
ilies. Figure 6 represents the essentials of his scheme. The
Blattidæ and the Mantidæ are entirely divided off as early as
the Carboniferous period. The stock from which·the other
groups have arisen was divided into two rather definite

divisions, one including the Phasmids and the Acrididæ with some others that are not being considered here for want of information concerning their habits, and the other the Locustidæ and the crickets.   The Gryllotalpinæ have arisen in comparatively recent times from the typical stock of the Gryllidæ.
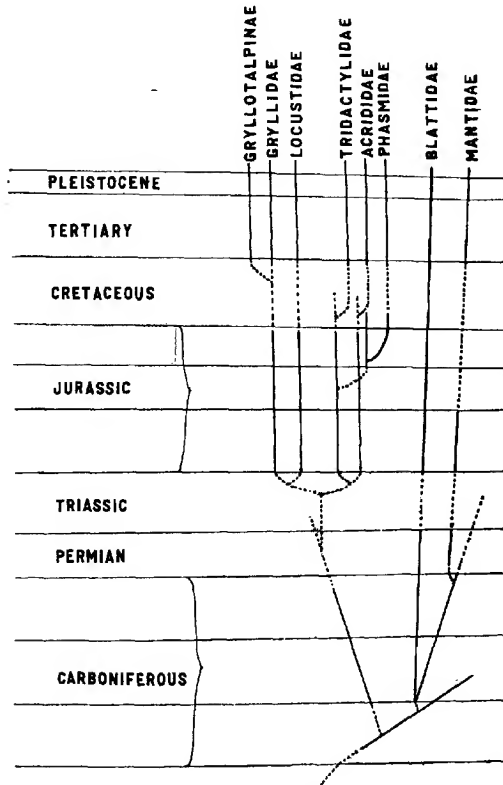

Fig. 6.   Scheme indicating the phylogeny of the Orthoptera.

A comparative study of Figures 5 and 6 suggests that the agreement between the diagrams is not a mere coincidence. From a common ancestral stock specialized types have arisen, some persisting and others perishing.   We may assume that

the variations arose, first, because the animals were subjected to a new environment and the necessary modifications in the behaviour caused modifications in structure, or that variations in structure arose by orthogenesis and the animals were called upon to find a suitable environment or perish.   The latter assumption seems to be the most reasonable.   The agreement between the two figures also suggests that the more fundamental modifications in structure and in behaviour have been fairly constant since their origin.

SUMMARY.

1.   Movements preliminary to copulation are fairly constant for each group of the Orthoptera and vary from very simple (Mantidæ, Phasmidæ and Acrididæ) to complex (Blattidæ, Gryllidæ and Locustidæ).

2.   There is a sex discrimination in the males of all forms. The female plays an aggressive part and displays a discrimination of sex in some groups while in others she is absolutely passive.

3.   There is a typical mode of copulation for each family of the Orthoptera.   In the Mantidæ, the Phasmidæ and the Acrididæ there is a superposition of the body of the male.   In the Blattidæ and the Gryllidæ there is a superposition of the body of the female.   In the Locustidæ there is an "end to end" copulation.

4.   Families represented by the least number of subfamilies are highly specialized while those represented by the largest number of subfamilies have a generalized type of reproductive behaviour.

5.   A comparison between a classification based upon the reproductive behaviour and one based upon pæleontological evidence shows a striking agreement and suggests that the different types of reproductive behaviour have been fairly constant since their origin.

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THE CLASSIFICATION OF THE PUPÆ OF THE SATURNIIDÆ.*

EDNA MOSHER.

A short discussion of the characters of the pupæ of the superfamily Saturnioidea was given in a preceding paper, Annals Entomological Society of America, Vol. VII, pp. 277-8, including a key for the separation of the three families. Two of the families, the Ceratocampidæ and Hemileucidæ were discussed in that paper, and the third, the Saturniidæ, will be considered here. Plate V, included in this paper shows some of the more important structures of the Ceratocampidæ and Hemileucidæ.

The general characters of the family Saturniidæ are as follows: Body with abdominal segments 5 to 7 capable of being telescoped, antennæ broadly pectinate throughout, or nearly so, the stem of the flagellum distinct and raised above the level of the pectinations, varying greatly in the sexes, always broader and usually longer in the male; maxillæ, measured on the meson,† never more than one-third the length of the wings; the exposed portion of the tibiæ and tarsi of the first pair of legs, and the tips of the second pair of legs with their lateral margins adjacent on the meson, never with the distal ends of the tarsi of the first and second pairs of legs meeting obliquely on the meson; first pair of wings with the anal angles broadly rounded, and always reaching the caudal margin of the fourth abdominal segment on the ventral surface; second pair of wings produced around the anal angles of the first pair of wings and usually forming prominent angles on the fourth abdominal segment, always extending at least a short distance along the ventral margin of the first pair of wings; metathorax without distinct oblong tubercles one-third or more the width of the segment; suture between the seventh and eighth abdominal segments never deep with distinct crenulations on its margins; distinct cremaster never present; pupæ always found in cocoons.

Of the family Saturniidæ, the pupæ of eight genera have been described in the following pages. They may be separated by the following key:

A. Body never cylindrical, but tapering gradually from the middle as in Fig. 13, the lateral margins of the movable segments never approximately parallel; caudal end of body usually with stout curved spines.

    B. Tenth segment never flattened into a transverse plate, with the caudo-lateral angles produced into short lobes.

        C. Caudal end of body without spines; body surface with slightly wavy, transverse ridges, with distinct furrows between; mesothorax never with a prominent tubercle at the base of each wing.   *Copaxa.*

       CC. Caudal end of body with stout, curved spines; body surface never with slightly wavy, transverse ridges with distinct furrows between; mesothorax with a prominent tubercle at the base of each wing.

            D. Lateral aspects of the cephalic margins of abdominal segments 5 to 7 never with sharp, slightly wavy, transverse ridges with distinct furrows between; caudal end of body with an oval area set with slightly curved spines, usually arranged in two groups and nearly all pointing outwards.   *Telea.*

          DD. Lateral aspects of the cephalic margins of abdominal segments 5 to 7 covered with sharp, slightly wavy, transverse ridges with distinct furrows between; caudal end of body deeply rugose, with a slight concavity containing a circular group of strongly recurved spines.   *Tropaea.*

     BB. Tenth segment, viewed dorsally, a transverse plate, concave on the caudal margin, the caudo-lateral angles produced into lobes, the segment strongly concave in ventral view, with five short, curved spines inserted close together in the caudo-lateral margin of each lobe.   *Agapema.*

AA. Body cylindrical in outline, as in Fig. 14, the lateral margins of the movable segments approximately parallel; caudal end of the body never with stout curved spines, but sometimes with short, straight ones.

    B. Maxillae, measured on the meson, always one-fourth or less the length of the wings, the proximal two-thirds of their margins never strongly concave; first pair of wings with their anal angles on the cephalic margin of the fourth abdominal segment or caudad of that portion of the segment.

        C. Maxillae, measured on the meson, less than one-fifth the length of the wings; antennae of males with the sides tapering gradually to a pointed tip.

            D. Both eye-pieces never visible in either sex; caudal end of abdomen never with a band of coarse setae, sometimes with a few very short, straight spines.

              E. Glazed eyepiece visible in both sexes; caudal end of abdomen with a few very short, straight spines.   *Eupackardia.*

             EE. Glazed eyepiece never visible in either sex; caudal end of abdomen never with short, straight spines.   *Callosamia.*

           DD. Both eyepieces visible in either sex; caudal end of abdomen with a transverse band of coarse setae. *Rothschildia*

       CC. Maxillae, measured on the meson, never less than one-fifth the length of the wings; antennae of males with the sides approximately parallel for the greater part of their length, tapering rapidly to a blunt, rounded tip; a small portion of glazed eyepiece always visible in the females.   *Samia.*

    BB. Maxillae, measured on the meson, always more than one-fourth' the length of the wings; the proximal two-thirds of the lateral margins of the maxillae concave; first pair of wings with their anal angles on the third abdominal segment, opposite the second pair of abdominal spiracles.   *Philosamia.*

Genus **Copaxa** Walker.

Body tapering at cephalic end; face parts scarcely elevated above the surface of the body; antennæ pectinate throughout, the stem of the flagellum slightly elevated above the pectinations; glazed eye-piece visible in the female; invaginations for the anterior arms of the tentorium distinct; clypeo-labral suture distinct; maxillæ, measured on the meson, about one-seventh the length of the wings; tarsi of the first pair of legs adjacent on the margin in the female, covered by the antennæ in the male; second pair of legs not visible; median thoracic line distinct, sometimes elevated on the prothorax, faint on the mesothorax and metathorax; caudal part of mesonotum and metanotum not depressed adjacent to wings; wings with their distal margins slightly elevated above the dorsal surface of the body; first pair of wings with their anal angles broadly rounded; second pair of wings visible around the entire dorsal margin of first wing and produced below the anal angle to form a prominent angle opposite the third abdominal spiracle, but not reaching the caudal margin of the fourth abdominal segment; abdominal segments 8 to 10 distinctly segmented, tapering rapidly to form a cone.

This genus is found in Mexico and southward. The cocoons are brown, composed of two layers and are much like those of *Agapema galbina*. The outer layer is very thin and coarsely reticulate, usually attached to a leaf. The inner layer is much thicker, finely reticulate, and the cocoon has an opening at the end, with loose fibers for the emergence of the moth.

Copaxa lavendera Westwood.— Color variable, usually yellowish brown to black, marked with darker brown, or dark brown to black, with traces of yellowish brown; face parts with fine, indeterminate longitudinal striations, appendages and wings with indeterminate transverse striations, remainder of body surface with slightly wavy, interrupted ridges, mostly transverse, with distinct furrows between; antennæ of male slightly raised above the level of the wings, the length about two and three-quarters times the width, the sides approximately parallel for the greater part of the length, tapering to a point at distal end and lying adjacent on the margin for a distance equal to its width; antennæ of female not raised above the level of the wings, the length three and one-half times the

width, tapering to a point at the distal end, the tips meeting on
the meson over the tips of the first pair of legs; labrum variable,
the width a little greater than the length, usually five or six
sided, slightly tuberculate, and broadly rounded or slightly
bilobed at the distal end; maxillæ triangular in outline or
somewhat heart-shaped, the median length slightly less than
the greatest width; spiracles free. Length, abdomen retracted,
30-32 mm., expanded, 33-35 mm., girth, 38-45 mm.

Genus **Telea** Hübner.

Body blunt at cephalic end; abdominal segments 1 to 4
rounded out above the margin of the body dorsad and forming
a distinct hump, segments 5 to 7 distinctly decreasing in size and
caudal margin of segment seven joining cephalic margin of
segment eight with only a slight indentation between; antennæ
pectinate throughout, varying greatly with the sexes, the stem
of the flagellum in both always less than one-third the total
width; eye-pieces not visible; invaginations for the anterior
arms of the tentorium distinct; clypeo-labral suture distinct;
maxillæ, measured on meson, about one-fourth length of
wings; legs in the male covered by antennæ, in the female
tarsi of first pair and tips of second pair adjacent on the meson;
median thoracic line carinate on all segments; mesothorax
with a prominent tubercle at base of wings;* caudal part
of mesonotum and metanotum depressed adjacent to the
wings; wings with their distal margin raised above the dorsal
surface of body; dorsal cephalic margins of abdominal segments
5 to 7 form a heavy raised line extending laterad and cephalad
of the spiracles to the proleg scars on the ventral surface;
abdominal segments 7 to 10 tapering rapidly, forming an oblique
convex cone-shaped piece; tip of abdomen with a small oval
area set with fifteen or more stout, black, slightly curved

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*Mesothoracic tubercles are found in the pupae of many genera, but are
especially prominent in the case of *Tropaea luna* and *Telea polyphemus* (Fig. 11,
w. t.), where at the proximal ends of the wings they differed so much in shape and
size from any others noticed in the study of pupae. that they were investigated
and each found to contain a prominent spine. This spine is used to cut the cocoon
to allow the imago to escape and was found in the imagos of all genera of Satur-
niidæ studied, but especially well developed in the genera previously mentioned.
A study of the preimago showed that this spine was an outgrowth from one of the
wing sclerites, the third axillary of Snodgrass. In *Telea polyphemus* (Fig. 12),
there is also a smaller spine cephalad of the large one.

spines, usually arranged in two small groups and nearly all pointing outwards.

This genus consists of a single species, *Telea polyphemus*, found in all parts of the United States. Their cocoons consist of a thick, firm layer, never "papery," like those of *Tropaea luna*. The cocoons are pale grayish tan in color, ovoid in shape, blunt at the ends and usually fastened between two leaves. It never has an opening at the end with loose fibers across it, as many cocoons have. It is found suspended from twigs where it often fastens the leaf to a tree and is also found on the ground among the fallen leaves.

Telea polyphemus Cramer (Figs. 11 and 13).—Color yellowish brown, with darker brown around margins of spiracles, and appearing at various places on surface as the age increases; face parts not elevated, always white between the antennæ, the white strip narrowing down to the proximal margin of the labrum and concave on its lateral margins; prothorax and mesothorax with faint transverse striations, remainder of body surface smooth, with the exception of longitudinal wrinkles on the metathorax and first abdominal segment and some slight dorsal impressions; antennæ of male five-sixths the length of wings on the meson, length twice the width; meeting on the meson for more than half their length; antennæ of the female two-thirds the length of wings on the meson, length three times the width, separated by the legs and ending slightly below tips of the first pair; labrum variable, tuberculate, generally five or six sided, the distal margin either slightly or deeply bilobed; maxillæ triangular in outline, the mesal length greater than greatest width; mesothorax with wing tubercles prominent, broadly elevated, with a distinct apex marked by an angular furrow on the caudo-mesal margin; first wing with its anal angle broadly rounded, below cephalic margin of fourth abdominal segment; margin of second wing entire in the female, slightly emarginate in the male, visible along entire dorsal margin of first wing, and produced below anal angle of first wing, extending about two-fifths of the distance across its caudal margin; mesothoracic spiracles with their cephalic margins strongly convex. Length, retracted, 25-35 mm.; expanded, 30-40 mm.; girth, about 50 mm.

Genus **Tropaea** Hübner.

Body usually somewhat depressed; abdominal segments
5 to 7 distinctly tapering, face parts never elevated above
the surface of the body; antennæ pectinate throughout, the
stem of the flagellum elevated above the level of the pecti-
nations and more than one-third the total width; invaginations
for the anterior arms of the tentorium distinct; eye-pieces
both visible; clypeo-labral suture distinct; maxillæ, measured on
meson, about one-eighth the length of wings; about half the
tibiæ and the tarsi of the first pair of legs and the tips of the
second pair of legs adjacent on the meson; median line distinct
on all thoracic segments; each mesothoracic spiracle about one-
fourth the distance along the caudal margin of prothorax to
meson; mesothorax with a prominent tubercle at base of wings
and a slight depression along lateral margin of alar area; caudal
part of mesonotum and metanotum not depressed adjacent to
wings; wings with their distal margins not elevated above the
surface of the body; abdominal segments 5 to 7 with the lateral
aspects of the cephalic margins covered with sharp, slightly
wavy, transverse ridges with distinct furrows between, the
cephalic margin narrowed on the dorsum, the furrows extending
dorsad about two-thirds of the distance between the spiracular
line and the meson and ventrad less than half way between the
spiracular line and the meson, the furrows usually concealed
when the abdomen is retracted; abdominal segments 8 to 10
tapering quickly to form a convex cone-shaped piece; caudal
end of body deeply rugose with a slight concavity containing
a circular group of strongly recurved spines, the curved tips
all pointing toward the center of the group.

This genus is found throughout the Atlantic States and the
Mississippi Valley, and includes a single species in this country.
The cocoon is ovoid, thin and "papery" on the outside, with a
thin inner layer of loose fibers of silk, but it has no opening
at the end with loose fibers of silk closing it, as in *Callosamia
promethea.*   The cocoon is usually brown in color, and is found
among the leaves on the ground under the food plant.

Tropaea luna Linnaeus.—Color generally chestnut brown
with an irregular white blotch extending between the proximal
ends of the antennæ; face parts and exposed portion of thorax
with fine indeterminate, impressed lines, the first eight abdom-

inal segments with fine punctures more numerous at the dorsal cephalic portion of segment; antennæ of male tapering gradually until near distal end, then the mesal margin concave to tip, length two and one-half times the width, ending near the middle of exposed portion of tarsus of the second pair of legs; labrum variable, usually broadest on the distal portion, with more than twice the length, five-sided and pointed at the distal end; maxillæ with each half quadrilateral, the median length much less than the greatest width; first wing with its dorsal margin rounded from point of attachment, so that the anal angle is almost impossible to determine; second wing visible around entire dorsal margin of first wing, its margin entire, not produced to form an anal angle and extending about half way across caudal margin of first wing.   Length, abdomen retracted, 30-37 mm., expanded, 37-45 mm., girth 38-50 mm.

Genus **Agapema** Neumoegen & Dyar.

Body tapering at cephalic end, abdominal segments 8 to 10 never forming a cone; antennæ pectinate throughout, tapering to a point at the distal end; invaginations for the anterior arms of the tentorium distinct; eye-pieces both visible; labrum elevated above the surrounding surface, clypeo-labral suture obsolete; maxillæ measured on meson about one-seventh the length of wings; median thoracic line distinct on prothorax and mesothorax, sometimes on the metathorax; strongly carinate on prothorax: caudal portion of mesonotum and metanotum slightly depressed at base of wings; wings with their distal margin slightly raised above the dorsal surface of body; lateral aspect of the cephalic margins of abdominal segments 5 to 7 with sharp, slightly wavy, transverse ridges with distinct furrows between, the cephalic margin narrowed on the dorsum and the furrows indistinct, furrows extending ventrad to the region of the proleg scars; cremaster absent; abdominal segments with distinct depressions between the segments, excepting on the dorsum; the tenth segment, as viewed from above, a transverse plate, concave on the caudal margin and the lateral angles produced into lobes, as viewed from ventral aspect, the ventral surface strongly concave and five short, curved spines inserted close together in the lateral margin of each lobe.

This genus includes a single species in North America, *Agapema galbina*, found in Arizona, Texas and Mexico. The pale grayish tan cocoons consist of two layers, a very thin, coarsely reticulated outer layer, and an inner thicker layer with smaller reticulations, both layers having loose fibers at the cephalic end closing an opening made by the thicker walls. It is suspended by the side, as *Samia cecropia*.

Agapema galbina Clemens.—Color generally tawny or yellowish brown, with slightly darker transverse conjunctiva and margins of spiracles; entire surface except wings and antennæ, covered with fine wavy impressed lines and coarse punctures; wings and antennæ with similar lines, but much deeper impressions; face parts elevated; tips of antennæ usually lie adjacent on the meson for a distance nearly equal their width, occasionally separated by the cases for the first pair of legs; length two and one-half times width, stem of the flagellum elevated above the level of the pectinations; labrum slightly longer than broad, its distal end rounded or pointed; maxillæ with each half somewhat triangular in outline, with lateral margins concave, surface almost smooth; space between maxillæ and antennæ filled in by part of the tibia and tarsus of the first pair of legs; mesothoracic spiracles triangular, mesothorax with lateral part of alar area elevated and a smooth, rounded spot about two-thirds of the distance from the cephalic margin; first wing with its anal angle very broadly rounded on cephalic margin of fourth abdominal segment; second wing visible along entire dorsal margin of first wing, its margin entire, produced around angle of first wing, but never reaching half way across its caudal margin; first and second abdominal spiracles often partially covered by the wings. Length, abdomen contracted, from 15-25 mm.; girth, 25 mm.

Genus **Callosamia** Packard.

Body cylindrical; face parts slightly elevated; antennæ pectinate throughout, tapering gradually to a point at the distal end, the stem of the flagellum raised above the level of the pectinations and one-third the total width of the antenna; invaginations for the anterior arms of the tentorium distinct; clypeo-labral suture obsolete; maxillæ, measured on the meson, always about one-sixth the length of the wings, triangular in outline; tarsi of the first pair of legs and tips of the second pair

adjacent on the meson; median line distinct on the prothorax
and mesothorax; caudal portion of mesonotum and the meta-
notum depressed adjacent to the wings; wings with their
distal margin always raised above the level of the dorsal surface
of the body; first pair of wings with their anal angles rounded
and opposite the cephalic margin of the fourth abdominal
segment; second pair of wings visible along entire dorsal margin
of first pair; abdominal segments 8 to 10 tapering rapidly
to form a cone; cremaster absent.

This genus includes two species in North America. Both
of these, *C. promethea* and *C. angulifera*, are found east of the
Mississippi. The cocoons of *C. promethea* resemble those of
P. walkeri, but are more common, dangling in clusters from
almost every spice bush, wild cherry and many other food
plants in regions where they occur. Promethea cocoons are
grayish brown in color, usually darker than walkeri cocoons
and cylindrical in shape, generally blunt at the caudal end.
They are suspended by a long band of silk from the cephalic
end which usually fastens the encircling leaf to a twig together
with the cocoon. *C. angulifera* is comparatively rare and
its cocoons are seldom found suspended from twigs, but are
usually found among fallen leaves at the base of a tree. They
are ovoid, dull brownish gray in color, with the valvular arrange-
ment of loose fibers of silk at one end. The walls of the cocoon
are thicker than promethea cocoons and more readily separated
into layers.

The following table will serve to separate the pupæ of this
genus:

A.   Dorsal cephalic margins of abdominal segments 5–7 produced into a
      flange-like ridge, widest at meson and ending opposite spiracles; spiracular
      openings at the bottom of a lenticular depression; dorsal margin of second
      pair of wings scarcely bisinuate.   *promethea.*

AA.   Dorsal cephalic margins of abdominal segments never produced into
      a flange-like ridge; spiracular openings with a lenticular, elevated, smooth,
      rounded margin; dorsal margin of second pair of wings deeply bisinuate.
                                                                    angulifera.

Callosamia promethea Drury.—Color generally yellowish,
dark brown on the middle of the back and around the margin
of spiracles, sometimes on the wings; dorsal aspect of thorax
and abdomen with deep, wavy, transverse striations, fine, inde-
terminate striations on face parts, wings and legs, the remaining
surface practically smooth; dorsal cephalic margins of abdom-

inal segments 5–7 produced into flange-like plates, widest at the meson and ending opposite the spiracles; line between segment and transverse conjunctiva elevated on dorsal aspect; tips of antennæ generally separated by second pair of legs, ending in the female half-way between the tips of the first and second pairs of legs, in the male. opposite the tips of the second pair, tips of antennæ in both sexes frequently meet on meson, those of male slightly longer and wider than those of female, the length never more than three times width; no eye-pieces visible; labrum variable, broadly rounded distally; maxillæ generally smooth, sometimes separated on meson to show coxal cases beneath, length on meson equals breadth at cephalic end; margin of second pair of wings scarcely bisinuate, produced into a rounded anal angle and extending less than half way across caudal margin of the first pair; mesothoracic spiracles small; first and second abdominal spiracles partially covered by the wings; spiracular openings located at the bottom of lenticular depressions, lips of the depression smooth and glossy, and of the opening, rounded and of a different color; abdominal segments 8–10 taper rapidly to form a cone, occasionally with a button-like tip. Length, abdomen retracted, from 20–30 mm., expanded, 25–35 mm.; girth about 40 mm.

Callosamia angulifera Walker.— Color generally yellowish or yellowish brown, darker brown on the middle of the back and around the margins of spiracles, usually a darker color pattern on wings; dorsal aspect of thorax and abdomen with deep, wavy, transverse striations, fine indeterminate striations on face parts and appendages, the remainder of the surface practically smooth; dorsal cephalic margins of abdominal segments 5–7 never produced into flange-like plates; line between segment and conjunctiva on dorsal aspect elevated and corrugated; antennæ of male meet on meson and lie adjacent to each other for a distance nearly equal to their width, their length three times the width, antennæ of female separated to show first and second pairs of legs, their length three and one-third times width, ending just below first pair of legs; no eye-pieces visible; labrum variable, usually broadly truncate distally; maxillæ with mesal length greater than breadth at cephalic end; margin of the second pair of wings deeply bisinuate, a narrow portion produced below anal angle of first

wing and extending less than half way across its caudal margin; first and second abdominal spiracles seldom partially covered by wings; spiracular openings with an elevated, rounded, smooth, lenticular margin, the lips of the openings rounded and pitted; tip of abdomen rounded. Length, abdomen retracted, 20–25 mm., expanded 25–30 mm.; girth, 40 mm.

Genus **Eupackardia** Cockerell.

This genus strongly resembles Callosamia, except for the points indicated in the key. The face parts are slightly elevated; antennæ pectinate throughout, the stem of the flagellum always elevated above the level of the pectinations and about one-third the total width; invaginations for the anterior arms of the tentorium distinct; clypeo-labral suture indicated by a slight furrow; maxillæ measured on the meson one-sixth the length of the wings; tarsi of the first pair of legs and tips of the second pair adjacent on the meson; caudal part of the mesonotum and metanotum depressed adjacent to the wings and strongly wrinkled, the wrinkles extending over the first two abdominal segments; wings with their distal margin always raised above the level of the dorsal surface of the body; first pair of wings with their anal angles rounded and opposite the cephalic margin of the fourth abdominal segment; second pair of wings scarcely visible opposite the second abdominal spiracle, but otherwise entirely visible around the first wing and extending below it on the ventral surface, reaching about half the distance along the caudal margin of the first wing; abdominal segments 8 to 10 tapering rapidly to form a cone-shaped piece; cremaster absent.

This genus includes a single species. *Eupackardia calleta* is reported from Arizona and Mexico. Its cocoon is very firm, flask-shaped, with loose fibers of silk forming a sort of valve across the open cephalic end. It is suspended from a twig by means of a very short band of silk which encircles the twig.

Eupackardia calleta Westwood.—Color generally dull black with a yellowish face-piece; exposed surface of thorax, face-pieces and appendages with fine indeterminate transverse striations, remainder of surface practically smooth; dorsal cephalic margin of abdominal segments 5 to 7 never produced into flange-like plates; never with an elevated line between the segment and the transverse conjunctiva; antennæ of female extends to tips of first pair of legs and length is four times

width, in the male they reach to tips of second pair and length is three and one-half times width; glazed eye-pieces visible; labrum variable, generally elevated, pentagonal or shield shaped; maxillae with mesal length and breadth at cephalic end approximately equal; margin of second wing slightly sinuate, produced below anal of front wing to caudal margin of fourth abdominal segment and more than half way across caudal margin of first wing; first and second abdominal spiracles partially covered by the wings; spiracular openings located at the bottom of lenticular depressions, margins of the openings felted; tip of abdomen rounded with ten or more short, rigid spines less than one millimeter long, forming a circular group. Length, abdomen retracted, 25–30 mm., expanded 35–40 mm.; girth about 50 mm.

Genus **Rothschildia** Grote.

Exposed surface of thorax and abdomen sparsely covered with fine setæ; face-parts slightly elevated; antennæ pectinate throughout, tapering gradually to a point at the distal end, length and width varying with the sexes and reaching more than half way between the tips of first and second pairs of legs; antennæ of male elevated, with a depression on each side the stem of the flagellum; antennæ of female with the stem of the flagellum raised above the level of the pectinations; invaginations for the anterior arms of the tentorium indistinct; eye-pieces both visible; clypeo-labral suture generally distinct; maxillæ, measured on meson, about one-fifth the length of wings, triangular in outline, its mesal length greater than the width at proximal end; tarsi of the first pair and tips of the second pair of legs adjacent on the meson; metanotum wrinkled at base of wings but not always depressed; wings with their distal margins raised above the dorsal surface; first wing with its angle on cephalic margin of fourth abdominal segment; second wing visible along dorsal margin of first wing, its margin entire and produced below the anal angle of first wing to the caudal margin of the fourth abdominal segment, extending more than half way across margin of first wing; spiracular line curves ventrad; cremaster wanting; abdominal segments 8–10 bluntly cone-shaped, the caudal end with a band of coarse setæ about one millimeter long, either erect or closely appressed to the body.

This genus consists of two species found in Arizona and southward into Mexico. The cocoons are very firm, those of *R. orizaba* being about two inches long, three-fourths of an inch wide, rather ovoid in shape, usually slightly narrowed and rounded at the ends, while those of *R. jorulla* are vase-shaped, about of the same dimensions with a well defined opening laterally at the cephalic end, showing the valvular arrangement of loose fibers. Both species have very light grayish tan cocoons, those of *R. jorulla* being suspended by a band of silk at the cephalic end. The pupæ of the two species can be separated as follows:

A.   Median thoracic line distinct on all segments; caudal part of meso-
     notum and metanotum depressed at base of wings; distal margin of wings
     strongly elevated above the dorsal surface of body; setæ on metathorax and
     first four abdominal segments sparsely distributed, inconspicuous. *orizaba.*

AA. Median thoracic line never distinct on metathorax and often indistinct on
     mesothorax; caudal part of mesonotum and metanotum not depressed at
     base of wings; distal margin of wings only slightly elevated above the
     dorsal surface of the body; setæ numerous on metathorax and first four
     abdominal segments, conspicuous, at least a millimeter in length. *jorulla.*

Rothschildia orizaba Westwood.—Color generally black with light brown transverse conjunctiva, sometimes abdominal segments 5-10 or 8-10 are light in color; exposed parts of thorax and abdomen sparsely covered with reddish setæ, less than a millimeter long and almost invisible; thoracic segments, face parts and appendages with indeterminate, transverse striations, abdominal segments smooth; antennæ of male with length two and three-fourths times breadth, female with length four times the breadth; face parts curving sharply to the level of the labrum and maxillæ; labrum variable, width about twice length, usually five-sided and slightly elevated above maxillæ; maxillæ, measured on meson, one-sixth the length of wings; median line distinct on all thoracic segments; mesothorax tuberculate at base of wings; caudal part of mesonotum and metanotum strongly depressed adjacent to wings; the distal margin of first wing always considerably elevated above the dorsal surface of body; mesothoracic spiracles slit-like; abdominal spiracles free, second abdominal spiracle one-half the width of.its margin away from the wing; caudal end of abdomen with band of stiff, straight setæ, always erect. Length, abdomen retracted, 23–27 mm., expanded, 30–37 mm.; girth about 50 mm.

Rothschildia jorulla Westwood.—Color usually reddish brown; exposed surface of thorax, and usually the face parts, with fine, indeterminate, transverse striations, deeper on the prothorax; abdominal segments 1–4 with minute tubercles, remainder of body surface practically smooth; exposed surface of thorax and abdomen with conspicuous, coarse reddish setæ, most numerous on the first four abdominal segments and sparsely distributed over the remainder; antennæ in both sexes separated by the legs and extending more than half way between the tips of the first and second pairs of legs, length in the male three times the breadth, in the female almost four times the breadth; face parts convex, mostly in the clypeal region; labrum variable, always broader than long and generally with a rounded median lobe; maxillæ, measured on meson, one-sixth the length of wings; median thoracic line distinct on prothorax and part of mesothorax; mesothorax roughened and metanotum longitudinally wrinkled at base of wings, but never noticeably depressed; distal margin of first wing only slightly elevated above dorsal surface of body; abdominal spiracles usually free, second abdominal spiracle adjacent to the wings; caudal end of abdomen with a narrow, transverse band of setæ, sometimes extending on dorsal surface of tenth abdominal segment, either erect or closely appressed to body. Length, retracted, 25–28 mm.; girth about 45 mm.

Genus **Samia** Hübner.

Body cylindrical; face parts slightly elevated; antennæ with the stem of the flagellum raised above the level of the pectinations, in the female the antenna is pectinate throughout, not prominently elevated above the surface of the wings, and tapering gradually to a pointed tip at the distal end, in the male strongly elevated above the surface of the wings, the sides approximately parallel for the greater part of their length and tapering gradually to a blunt, rounded tip at the distal end, the stem of the flagellum often extending beyond the pectinations; a portion of the glazed eye-piece always visible in the female, sometimes in the male; invaginations for the anterior arms of the tentorium distinct; clypeo-labral suture usually distinct; labrum with width always much greater than length; maxillæ, measured on meson, never less than one-fifth the length of wings, triangular in outline, and usually smooth in comparison

with the other appendages, occupying a more or less sunken area between the elevated face parts and the first pair of legs; tarsi of the first pair of legs and tips of the second pair of legs adjacent on the meson; median line always very distinct on the prothorax, weak on the mesothorax and sometimes slightly indicated on the metathorax; caudal portion of mesonotum and the metanotum depressed adjacent to the wings; wings with their distal margins always strongly raised above the dorsal surface of the body; first pair of wings with their anal angles rounded and opposite the cephalic margin of the fourth abdominal segment; second pair of wings visible along entire margin of first wing, but usually almost concealed by the first wing on the third abdominal segment and produced around the anal angle of first wing to the caudal margin of the fourth abdominal segment; abdominal segments usually with three rows of tubercle scars on each side the meson, one row situated laterad of the dorsal medial line about one-fourth the distance between the medial line and the spiracular line, the second row on the dorsum about half way between the first row and the spiracular line, the third row on the ventral surface, not quite half way between the spiracular line and the proleg scars; abdominal segments 8–10 tapering rapidly to form a cone.

The genus *Samia* is found in nearly all parts of North America. There are four recognized species in this genus, *S. cecropia*, reported from the entire region east of the Rocky Mountains, *S. gloveri*, from the Rocky Mountain region and Arizona, S. columbia, from the Northern Atlantic States, and *S. californica*, from the Pacific States. The cocoons are always fastened by one side to a twig with fibers of silk; the general shape is oval. Cecropia cocoons are large, the largest found in North America, usually at least three inches long with two distinct layers of silk. There are many different shapes and at least two distinct types of cocoons, those with a very loose, soft outer layer giving the cocoon a "baggy" appearance and those firmer on the outside which are seldom more than an inch in width, often only three-fourths, while the "baggy" ones usually reach a width of two inches or even more. No satisfactory explanation has been given for this variation. The cocoons of the other species are similar to those of *S. cecropia* but smaller and usually firm. The cocoon of *S. gloveri* may usually be recognized by its external coating of white silk, which is spun first

by the larva. The other species usually have grayish-tan or brown cocoons. The pupæ of these species may be separated by the following table:

A. Dorsum of abdominal segments finely deeply rugose, glossy, somewhat resembling velvet; color usually very dark brown or black.
    B. Ventral row of tubercle scars always present and conspicuous, usually smooth and shining; tubercle scars on the metathorax and first abdominal segment very prominent and often red in color.
                                                             gloveri.
    BB. Ventral row of tubercle scars never present; tubercle scars on the metathorax and first abdominal segment small and inconspicuous and never red in color.   *californica.*
AA. Dorsum of abdominal segments finely rugose, but not deep enough to give the dull surface a velvety appearance; color usually yellowish or chestnut brown, rarely black.
    B. Maxillae one-fifth the length of the wings; length normally over one inch.   *cecropia.*
    BB. Maxillae one-fourth the length of the wings; length not over one inch; tubercle scars of the metathorax and first abdominal segments usually prominent, often elevated and tipped with red. *columbia.*

Samia californica Grote.—Color variable, typical specimens black, the caudal abdominal segments often light brown or yellowish and occasional specimens almost entirely yellowish brown; face parts, appendages and exposed surface of the thorax with fine, wavy, indeterminate transverse striations; dorsal abdominal segments 1–8 finely, deeply rugose resembling velvet, glossy in appearance, remainder of surface practically smooth; antennæ of male with the stem of the flagellum about one-fourth the total width of the antenna and with the tips sometimes extending beyond the pectinations; the length of the antenna a little more than twice the width and almost reaching the tips of the second pair of legs, the distal half of each antenna occasionally lying adjacent on the meson; antennæ of female with the stem of the flagellum one-third or more the total width of the antenna, ending opposite the tips of the first pair of legs and slightly shorter in some abnormal specimens, length a little more than three times width; clypeo-labral suture usually distinct; the clypeus not prominently convex cephalad of the labrum; labrum variable, concave on its proximal margin, broadly rounded or slightly pointed at distal end, the width at least twice the length; maxillæ, measured on meson, about one-fourth the length of wings, the mesal length usually greater than the greatest width; third pair of legs often showing between the wings; mesothorax with the alar area slightly polished, never showing a distinct tubercle or tubercle scar; metathorax without distinct tubercles; second pair of wings visible

around entire dorsal margin of first pair of wings, and seldom
concealed by them on the third abdominal segment, produced
below the anal angles of first pair of wings to the caudal margin
of the fourth abdominal segment; spiracles usually free, the
first and second seldom partially covered by the wings; abdom-
inal segments with the two dorsal rows of tubercle scars
generally distinct, but never having the row on the ventral
surface between the spiracular line and the proleg scars; abdom-
inal segments 5–7 with their dorsal cephalic margins produced
into narrow flange-like plates extending laterad to the spiracular
line, with a distinct notch at meson and the median line indi-
cated by oblique striations, also with a raised, wavy line between
the segment and the transverse conjunctiva; abdominal seg-
ments 8–10 with the caudal end produced into a narrow blunt
tip; the scars of the anal prolegs never distinct on each side the
anal plate; cremaster absent.   Length, abdomen retracted,
30–35 mm., expanded, 40–45 mm.; girth about 50 mm.

Samia cecropia Linnaeus.--(Figs. 8, 9, 10).   Color variable,
usually chestnut brown with black on thorax and appendages,
sometimes yellowish brown, but never entirely black; face
parts, appendages, and exposed surface of thorax with fine,
indeterminate, transverse striations, dorsal abdominal segments
1–8 finely rugose, but dull in appearance, not resembling velvet,
remainder of surface practically smooth; antennæ of male with
the stem of the flagellum about one-fourth the total width of the
antenna and always extending beyond the pectinations, the
length of the antenna about two and one-half times the width
and almost reaching the tips of the second pair of legs; antennæ
of female with the stem of the flagellum at least one-third the
total width, the length of the antenna about three and one-half
times the width and never extending as far as the tips of the first
pair of legs; clypeo-labral suture generally distinct, clypeus
prominently convex cephalad of the labrum; labrum concave
on its proximal margin, broadly rounded at distal end, the
width more than twice the length; maxillæ, measured on
meson, about one-fifth the length of the wings, length and width
approximately equal; third pair of legs very rarely showing
between the wings; mesothorax with the alar area polished,
usually showing a distinct tubercle or tubercle scar; meta-
thorax without distinct tubercles; second pair of wings usually
visible around entire dorsal margin of first wing, often almost

concealed by first wing on the third abdominal segment and produced below the anal angle of first wing to the caudal margin of the fourth abdominal segment; spiracles usually free, the first and second sometimes partially concealed by the wings; abdominal segments with the three rows of tubercle scars distinct; abdominal segments 5–7 with their dorsal cephalic margins very rarely produced into flange-like plates and these scarcely visible in lateral view, and elevated, longitudinally striate, wavy line between the segment and the transverse conjunctiva; abdominal segments 8–10 with the caudal end seldom produced into a narrow, blunt tip; in ventral view the scars of the anal prolegs usually distinct on each side of the anal plate; cremaster absent. Length, abdomen retracted, 32–35 mm., expanded, 40–45 mm.; girth about 55 mm.

Samia columbia Smith.—Color usually dark brown to blackish; face parts slightly elevated; face parts, exposed surface of thorax and dorsal surface of abdomen with fine, determinate, transverse striations, specially marked on the mesothorax, metathorax and face pieces; antennæ of male with the stem of the flagellum about one-third the total width of the antenna, and not extending beyond the pectinations, the length of the antenna about two and three-quarters times the width, ending opposite the tips of the first pair of legs; clypeo-labral suture usually distinct; clypeal region strongly elevated, mound-like, above the labrum; labrum variable, its proximal margin concave, width at least twice length, the distal margin broadly rounded; maxillæ, measured on meson, one-fourth the length of the wings, its mesal length usually greater than greatest width, the surface polished; third pair of legs very seldom visible between the wings; mesothorax with the alar area longitudinally rugose throughout, appearing somewhat polished to the unaided eye; metathorax with a prominent tubercle on each side the meson, a smaller one near each lateral margin, both tubercles reddish at tip; a similar pair usually present each side the meson on the first abdominal segment; second pair of wings not visible around entire dorsal margin of front wing being covered by the first pair of wings between the first and third abdominal spiracles; abdominal segments with the three rows of tubercle scars present and conspicuous; abdominal segments 5–7 sometimes with indications of a flange-like plate notched at the meson but never extending as far laterad as the

spiracular line, the caudal margin scarcely elevated adjacent to the conjunctiva; spiracle of the third abdominal segment and sometimes of the second partially covered by the wings; tip of abdomen usually slightly produced into a blunt tip; the scars of the anal prolegs seldom distinct on each side the anal plate; cremaster absent. Length, abdomen retracted, 23–26 mm., expanded, 26–30 mm.; girth about 35 mm. Described from male specimens only.

Samia gloveri Strecker.—Color variable, usually dark brown to black with traces of yellowish brown; face parts, appendages and exposed surface of thorax with fine, indeterminate transverse striations, abdominal segments finely, deeply rugose, usually velvety in appearance; antennæ of male with the stem of the flagellum about one-fourth the total width of the antenna, the stem of the flagellum projecting slightly beyond the pectinations, and extending almost to the tips of the second pair of legs, the length about two and three-quarters times the breadth; antennæ of female with the stem of the flagellum about one-third the total width of the antenna, extending to the tips of the first pair of legs, the length four times the width; clypeus not prominently convex above the labrum; labrum variable, seldom concave at proximal end and, if concave, only slightly so, width greater than length and broadly curved at distal end; maxillæ, measured on meson, between one-fourth and one-fifth the length of wings, seldom smoother than the other appendages, the median length and greatest width approximately equal; mesothoracic spiracles partially covered by antennæ; mesothorax with alar area polished; second pair of wings never visible around entire dorsal margin of the first pair of wings, but concealed by the first pair of wings between the first and third abdominal spiracles; metathorax without prominent tubercles, a prominent, usually reddish tubercle scar on each side the meson, and a small tubercle near each lateral margin of the metathorax; abdomen with three rows of tubercle scars, conspicuous and polished; cephalic margins of abdominal segments 5–7 with indications of a flange-like plate near the meson, the edges of the segment adjoining the transverse conjunctiva longitudinally ridged but scarcely elevated; first and second abdominal spiracles partially concealed by the wings; abdominal segments 8–10 with the caudal end produced into a narrow

blunt tip, in ventral view the scars of the anal prolegs distinct on each side the anal plate; cremaster absent. Length, abdomen retracted, 30–35 mm., expanded, 35–40 mm.; girth, 45–50 mm.

Genus **Philosamia** Grote.

Face parts slightly elevated; antennæ pectinate throughout, tapering gradually to a point at the distal end, the stem of the flagellum distinctly raised above the level of the pectinations and nearly one-third the total width of the antennæ, similar in the sexes; glazed eye-pieces visible in both sexes; invaginations for the anterior arms of the tentorium distinct; clypeo-labral suture indistinct; maxillæ, measured on the meson, about one-third the length of the wings; tips of first and second pairs of legs adjacent on the meson; median thoracic line distinct on all segments; caudal part of mesonotum and metanotum depressed adjacent to wings; wings with their distal margin raised above the dorsal surface of the body; first wing with its anal angle broadly rounded, opposite the second abdominal spiracle; second wing generally visible along the entire dorsal margin of first wing, its margin wavy, produced into a prominent anal angle reaching the caudal margin of the fourth abdominal segment; abdominal segments 8–10 tapering rapidly to form a blunt or truncate cone; cremaster absent.

This genus contains a single species, *Philosamia walkeri*, which is a native of China and was introduced into America from Europe. At first it was confined to the Atlantic Coast States, but is gradually spreading westward. The cocoons are on an average two inches long, half an inch wide and pointed at the caudal end. The cephalic end is open with a valvular arrangement of loose fibers of silk. The cocoons are encased in a leaf and suspended from the twigs by a band of silk spun over the petiole of the leaf holding it to the stem. The cocoons are pale gray or grayish tan in color and closely resemble the cocoons of *C. promethea*.

Philosamia walkeri Felder.—(Fig. 14). Color generally yellowish brown, darker on wings and dorsum; exposed surface of thorax and abdomen with fine, indeterminate, transverse striations; antennæ reaching half way between the tips of the first and second pair of legs; labrum short and broad, its width usually six times the length; maxillæ triangular in outline,

lateral margin with the proximal two-thirds concave; abdominal segments with a heavy, raised, slightly wavy line on the dorsal and lateral aspects of the caudal margin, extending ventrad to the proleg scars, a similar line along the cephalic margin ending opposite the spiracles; two dorsal rows of tubercle scars as in *Samia*.   Length, abdomen retracted, from 20–30 mm., expanded, 25–35 mm.; girth about 40 mm.
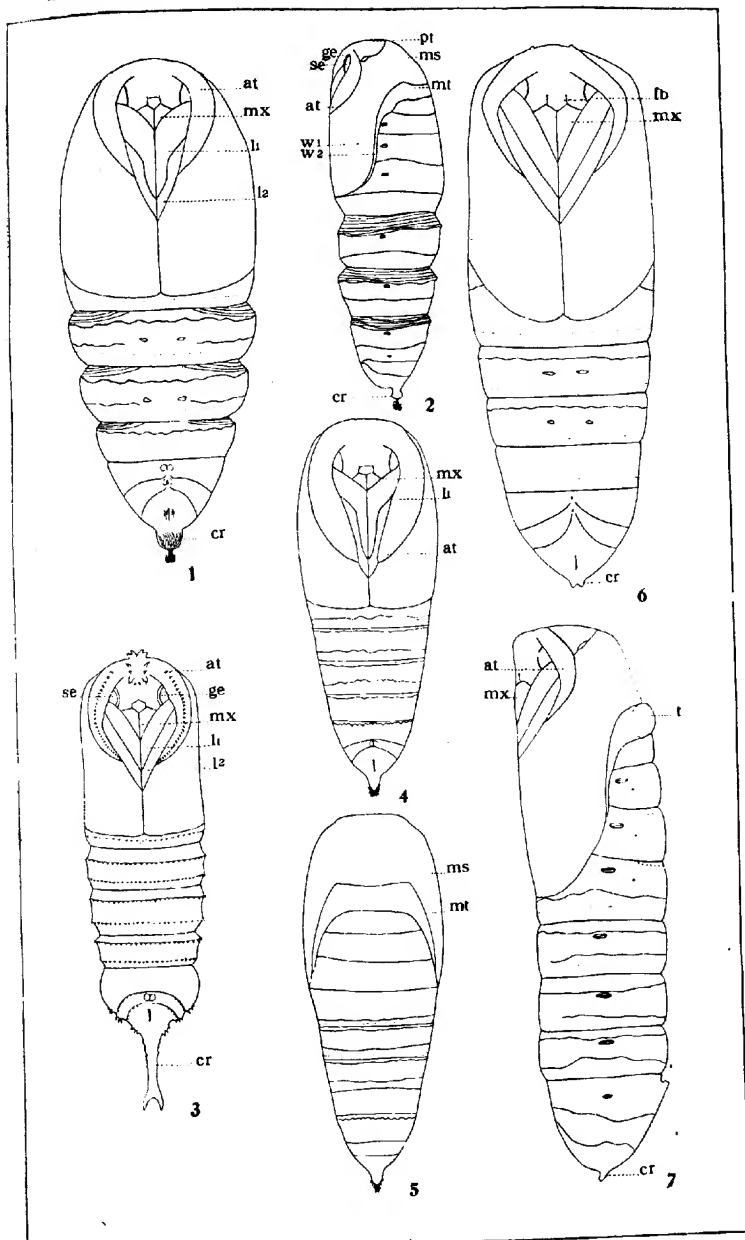

EXPLANATION OF PLATES.

PLATE V.

Fig. 1.   Ventral view of a pupa of Automeris io.
Fig. 2.   Lateral view of a pupa of Automeris io.
Fig. 3.   Ventral view of a pupa of Adelocephala bicolor.
Fig. 4.   Ventral view of a pupa of Hemileuca maia.
Fig. 5.   Dorsal view of a pupa of Hemileuca maia.
Fig. 6.   Ventral view of a pupa of Citheronia regalis.
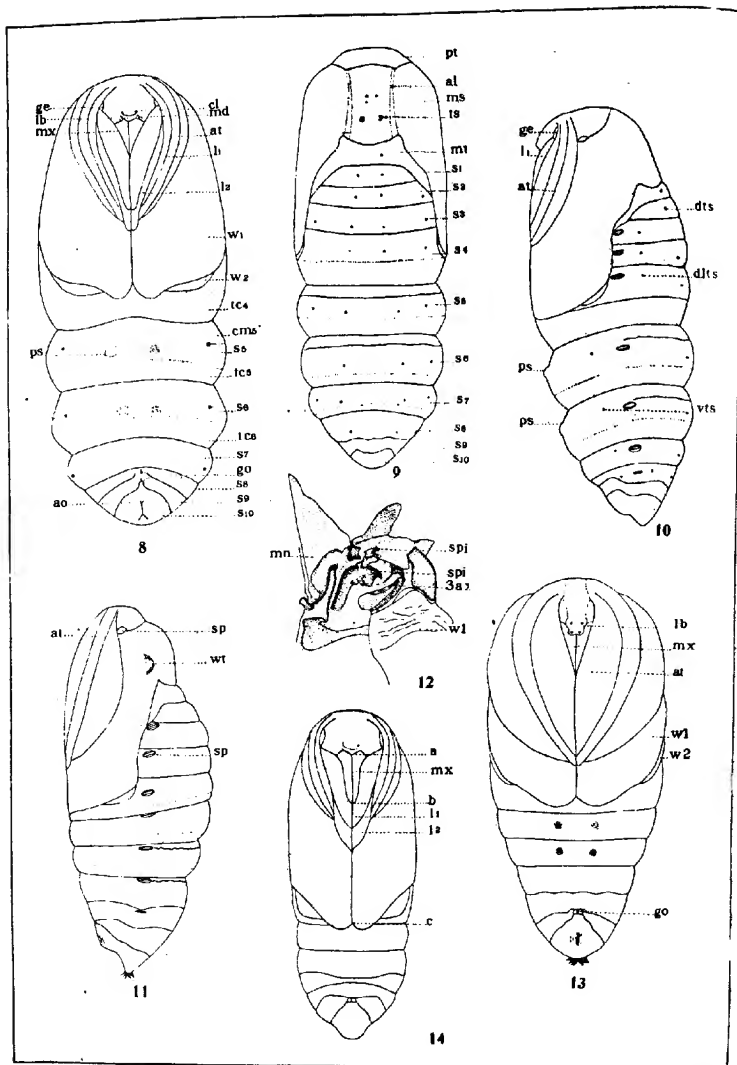Fig. 7.   Lateral view of a pupa of Citheronia regalis.

PLATE VI.

Fig. 8.   Ventral view of a pupa of Samia cecropia.
Fig. 9.   Dorsal view of a pupa of Samia cecropia.
Fig. 10.   Lateral view of a pupa of Samia cecropia.
Fig. 11.   Lateral view of a pupa of Telea polyphemus.
Fig. 12.   Wing sclerites of Telea polyphemus showing spines.
Fig. 13.   Ventral view of a pupa of Tela polyphemus.
Fig. 14.   Ventral view of a pupa of Philosamia walkeri.

ABBREVIATIONS.

al—alar area
ao—anal orifice.
at—antenna.
ax—axillary sclerite.
cl—clypeus.
cm—cephalic margin.
cr—cremaster.
dts—dorsal tubercle scar.
dlts—dorso-lateral tubercle scar.
ge—glazed eye.
go—genital orifice.
l—leg.
lb—labrum.
md—mandible.
mn—mesonotum.

ms—mesothorax.
mt—metathorax.
mx—maxillæ.
ps—proleg scar.
pt—prothorax.
s—segment.
se—sculptured eye.
sp—spiracle.
spi—spine.
t—tubercle.
tc—transverse conjunctiva.
vts—ventral tubercle scar.
w—wing.
wt—wing tubercle.

CONTRIBUTION TO THE BIOLOGY OF CERTAIN AQUATIC LEPIDOPTERA.*

PAUL S. WELCH.

Insects of the order Lepidoptera are so pre-eminently terrestrial in organization and habit that the existence of aquatic species is not commonly known, even among biologists. Information concerning American forms which inhabit the water is meager and only a few of their remarkable adaptations have been described. Klapálek and Grünberg ('09, pp. 96–159) discuss sixty species and varieties, which they consider as aquatic, from the fresh waters of Germany and there is reason to believe that ultimately the American aquatic species will be found to exceed that number. During the summers of 1911–15 the writer made some studies of the Lepidoptera of Northern Michigan in connection with which special attention was given to the aquatic group. The data, which form the basis of this paper, were secured in the immediate vicinity of Douglas Lake, in the extreme northern part of the Southern Peninsula. Certain portions of the margins of this lake are rich in aquatic vegetation and afford good breeding grounds for a considerable variety of aquatic animal life. Adults of five species of the genus *Nymphula* (Welch, '15, p. 118) were found in some abundance about the protected bays and beach pools. This genus is unique in being one of the very few groups of Lepidoptera which include species having aquatic stages in the life history. Of the species of *Nymphula* known to occur in North America, six are aquatic in some or all of the immature stages. The larvæ of several other species are not known, but it is probable that they, too, will be found to be aquatic.

In the past, generic divisions have been made in the group of species now included under *Nymphula*, based mainly on certain structural characters of the larvæ. Those species having tracheal gills in the larval stage were assigned to a separate genus, *Paraponyx*, a name still retained by some foreign workers. In this paper, the writer follows the present American practice of including the group assigned to *Paraponyx*, together with others, under the genus *Nymphula*. even though two distinct types of larvæ are thus involved.

Nymphula maculalis Clemens.

Nymphula maculalis occurred in some abundance in the immediate vicinity of the yellow water-lily beds and the writer was able to observe the development of this species, both in the field and in the aquaria, from the egg to the adult several times during the five successive summers, thus establishing the identity of the following described immature stages.

THE EGG (Pl. VII, Fig. 5).

The eggs were first described by Forbes ('10, p. 221) as follows: "*Eggs* were laid in captivity, but not in a regular egg-mass. They were oval and flattened, .65 by .5 mm., and had no decided longitudinal ridge. Duration of stage about ten days." This meager description, which seems to be the only one that has been published, contains no hint of the very interesting method of deposition under natural conditions. The writer made a careful study of this part of the life history and the results will be given in some detail.

Place and Method of Deposition.—Eggs were found only on the yellow water-lily, *Nymphæa americana* (Provancher) Miller & Standley. Other aquatic and semi-aquatic plants growing in the vicinity of the yellow water-lily beds were examined carefully but no eggs were found on them. They are laid ·on the lower side of the floating water-lily leaf and are thus constantly submerged.

Oviposition is associated in a very interesting and unique way with the deposition of the eggs of another aquatic insect. During the past five summers, the writer found about one hundred egg masses of *N. maculalis* in the field and, without exception, all were deposited in the manner to be described. A species of chrysomelid beetle (*Donacia* sp.), which occurs in considerable abundance about the water-lily beds of Douglas Lake, deposits its eggs on the lower surface of the leaves of the yellow water-lily in a very characteristic way. The female cuts a circular hole, 4–6 mm. in diameter, through the leaf and then, by means of a long ovipositor, lays two concentric rows of white, elliptical eggs around the margin on the lower surface. These concentric rows are very rarely complete, so that there may be two or more groups of eggs around the hole with varying intervening spaces. The interesting thing is the fact that the female

of *N. maculalis* uses the holes made by *Donacia* sp. for the depo-
sition of her eggs, thus taking advantage of the work of the
female beetle. The eggs of *N. maculalis* are laid in concentric
rows on the lower surface of the leaf, about the circular hole
and occupy space not utilized by the eggs of *Donacia*. Recently
deposited eggs of both beetle and moth were frequently found
about the same hole, showing that oviposition by the former is
sometimes followed shortly by egg deposition by the latter.
Recently deposited eggs of *N. maculalis* were occasionally found
about the egg holes of *Donacia* from which the eggs of the latter
had disappeared. The number of concentric rows of *N.
maculalis* eggs varies slightly but in the larger egg masses there
are six. The eggs are so placed that the long axes are radial
with reference to the hole about which they occur. The number
of eggs in a cluster varies rather widely. Frequently, the size of
the cluster is determined by the amount of space unoccupied by
the eggs of *Donacia*. In a few instances, the egg mass com-
pletely surrounded a *Donacia* egg hole, eggs of the latter being
absent. An examination of a large quantity of these egg masses
showed that the number of eggs in each varied from twenty-two
to two hundred eighty.

The act of oviposition was not observed and exact data on
this activity are lacking. However, the necessities make it
possible to draw tentative conclusions. The female of *N.
maculalis* has no means of making a hole through the leaf and,
since the eggs are laid in the above-described manner, she uses
the holes provided by some other agency. Even though the
writer has failed, in the collections of five summers, to find a
single egg mass in the field which was not associated with the
egg holes of *Donacia*, it seems improbable that the female
N. maculalis is restricted to them for egg deposition. In the
region examined, *Donacia* is the only animal which makes a
small, symmetrical hole through the leaf, a fact which may
account for the constant relation between the egg-laying habits
of the two species. Similar holes of different origin, if present,
might also be used. Since in most of the egg masses there are
six concentric rows so arranged that the row most remote from
the margin of the hole is four or five millimeters away, the
question arises as to the means whereby the female is able to
deposit eggs at such a distance from the edge of the hole. An
examination of the females of *N. maculalis* shows that the ter-

minal abdominal segment is elongated, cone-shaped, movable, bent ventrad, and bears a long, protrusible ovipositor. Thus it is possible for the female to deposit eggs from the top of the leaf by clinging at the margin of the hole and extending the ovipositor around the edge to the lower surface of the leaf. It also appears that the sixth concentric row of eggs in an egg mass represents the limit of extension of the abdomen and ovipositor.

A number of experiments were performed in order to secure further data on egg deposition. In each experiment, a single female, fresh in appearance and bearing evidences of recent emergence from the pupa, was captured in the field, brought to the laboratory, and placed in a well-lighted aquarium in which a yellow water-lily leaf, bearing no *Nymphula* eggs but having one or more *Donacia* egg holes, was floated on water. Frequent examinations were made of each aquarium during the day and the early part of the night. The results, based upon a number of such experiments, are as follows:

(1) Deposition of eggs invariably occurred at night.
(2) Eggs were deposited only about the *Donacia* egg holes.
(3) A female may deposit eggs for five successive nights before oviposition ceases.
(4) *Donacia* egg holes, devoid of *Donacia* eggs, were sometimes completely surrounded by six concentric rows of eggs of *N. maculalis.*
(5) An egg mass, deposited during one night, was sometimes covered, in part, by a second layer of eggs deposited on a succeeding night. Apparently, the deposition of one egg mass on another was an abnormal action, due, possibly, to laboratory conditions, although, aside from the limited space, the conditions in the aquarium resembled those of the natural environment as nearly as possible. Egg masses collected in the field invariably showed but a single layer. It is conceivable that such a reaction might result from the total reduction of available space about the *Donacia* egg holes, but experiments showed that it occurred when the same leaf contained holes which afforded abundant space.
(6) A single female usually utilized several *Donacia* egg holes before the egg laying period ended.
(7) The maximum number of eggs laid by a single female was 617.

The method of egg deposition in the absence of *Donacia* egg holes was of interest in this connection. Fresh, vigorous females, captured in the field, were placed in aquaria under conditions simulating the natural ones as nearly as possible. Each aquarium contained yellow water-lily leaves representing one of the following conditions: (1) entire leaves containing no *Donacia* egg holes; (2) leaves containing artificial holes, varying from narrow slits to circular holes, all of various dimensions; (3) pieces of leaves containing no holes and having smooth-cut

edges; and (4) ragged leaves and fragments of leaves with very irregular edges but no holes of any sort.

The results of these experiments were as follows:

(1) Most of the females tested with entire, unpunctured leaves delayed oviposition until the second or third night and then laid diminutive egg masses on the lower surface of the leaf near the margin, particularly in the region of the leaf sinus.

(2) Egg masses were deposited around artificial incisions and punctures of various kinds and shapes.

(3) Apparently, the dimensions of artificial punctures and incisions played little or no part in determining the location of egg masses.

(4) In the absence of leaf punctures, egg masses were deposited near the edges of smooth-cut portions of leaves, on the lower surface; also about the irregular edges of ragged and mutilated leaves.

It is evident from field observations and the above-described experiments that the female of *N. maculalis* has a distinct preference for the egg holes of *Donacia* in oviposition and that when present they are constantly utilized. However, in spite of the fact that, in the Douglas Lake region, the eggs are normally and constantly placed as above described, it is evident from the experiments that the dependence upon the presence of *Donacia* egg holes is not absolute and it seems fair to assume that in case *N. maculalis* occurs in a locality where *Donacia* egg holes or similar leaf punctures are absent, egg masses would be deposited about the leaf margins of the food plant. Observations on the egg-laying habits of *N. maculalis* in other parts of the continent would be of interest in this connection. This moth is widely distributed, having been reported from localities ranging from the Gulf States to Central Canada. Species of *Donacia* are said to occur in all parts of the United States and Canada and, although not all of them lay their eggs around circular holes in water-lily leaves, it appears that at least one of the rather widely distributed species does have this habit. The extent of this egg-laying interrelation of the two groups of insects is a problem for the future.

Description.—The eggs are elliptical, smooth, slightly compressed, and constant in size. When first hatched, the maximum dimensions are 0.396 mm. and 0.549 mm. The development of the egg is accompanied by an increase in size so that just before hatching the dimensions are 0.450 mm. and 0.648 mm. Of the considerable number of measurements made, none varied more than 0.03 mm. and even this variation was exceptional. It will be noticed that measurements of the egg made

previous to the time of hatching agree quite closely with those reported by Forbes ('10, p. 221). Apparently his measurements were made on eggs which were well advanced in development.

Development.—The egg period was found to be about eleven days, a result which agrees closely with that reported by Forbes. When first laid, the eggs are yellowish, having about the same color as the lower surface of the yellow water-lily leaf. They are also slightly translucent. As development goes on they become darker and proportionately more conspicuous on the leaf. During the first 2–4 days following oviposition, little if any change is apparent but subsequently internal differentiation becomes noticeable. The eggs develop uniformly and usually after a lapse of 3–5 days each begins to show a dark band within, shaped somewhat like the letter J. The position of this dark band is constant, the more curved end being in that extremity of the egg remote from the margin of the hole in the leaf. This band gradually becomes more conspicuous, ultimately revealing itself as the developing body of the larva. The triangular, chitinized pieces of the epicranium begin to appear at the end of the fifth day and it was noted that they develop in that end of the dark band nearest the margin of the leaf puncture, showing that there is a definite orientation of the egg and that the head of the larva develops at the less curved end of the band. At the close of the eighth day, the larva is quite distinct and occupies practically all of the space within the egg. At the end of about ten days, the egg has lost all of the original yellow appearance and the shell has become transparent. The tiny caterpillar can be easily examined and it begins to show movements within the egg. The primary regions of the body are now distinct (Fig. 4), the epicranium and the tips of the mouth parts are dark brown, the fronto-clypeal and the occipital regions are light yellow in appearance, and the chitinized, dark brown prothoracic shield and the dark bands in the regions of the intersegmental grooves are distinctly visible through the egg shell. In the eggs studied in this connection, the dark color appeared first in the ocelli and on the dorsal margins of the intersegmental grooves, later in the head and prothoracic shield. The larva is doubled upon itself with the caudal end extending around and beyond the head.

Hatching.—In almost every case, the entire egg mass hatched at about the same time. Occasionally, a few eggs lagged behind but they hatched not later than five hours after the main group of caterpillars had emerged. The first observed manifestations of the hatching process were motions of the larva within the egg, consisting of a series of body contractions and expansions combined with movements of the head. The mandibles were also in active motion. Apparently, the combined action of the mandibles and the body movements were responsible for the breaking of the egg shell. In the egg masses under observation, the movements of the larvæ preliminary to hatching began from four to six hours before the final escape. The larva emerged from one end of the egg, escaped quickly, and assumed an active habit. In egg masses deposited under natural conditions, the number of imperfect eggs was very small, not exceeding three per cent.

The dates of collection of egg masses varied from July 10 to August 20. Possibly, differences of seasons have some influence on the egg-laying period since in 1913 numerous egg masses were found as late as August 20, while during the preceding summer none were found later than July 30.

THE LARVA (Pl. VII, Figs. 1–3).

First Instar.—The first instar has been briefly described by Forbes ('10, p. 221) as follows: "*Stage I* (. . . . . . .)
Slightly larger than N. gyralis? described below, with proportionately much larger anal setæ, without trace of gills. Head nearly .3 mm.; length of large anal setæ 1 mm." A careful study of this instar has made it possible to extend the description.

The larva, in this instar (Fig. 1), is light yellowish brown in general appearance. The body is elongate, subcylindrical, and tapers very slightly caudad. Body length of newly hatched larvæ varied from 1.26 to 1.5 mm. The maximum diameter is in the region of the prothorax where it is about 0.32 mm. The main divisions of the body and the intersegmental grooves are distinctly marked. Duration of first instar in specimens reared in aquaria, about 7 days.

Head approximately 0.3 mm. in width, smooth, shining, and dark yellowish brown. Epicranial suture distinct. Front, clypeus and labrum light yellow. Labrum emarginate, setose.

Mandibles toothed, tips blackish. Labial palpi distinct, penultimate segment truncate-conic, ultimate segment smaller and cylindrical, not more than twice as long as thick, terminating distad in three short, stout spines. Maxillary palpi minute and inconspicuous, terminating in three minute articles. Antennæ distinct, basal joint truncate-conic, second segment slender, cylindrical, about three times as long as thick; distal extremity with an apical seta nearly twice as long as segment bearing it, and four minute articles, one of which bears a short seta. Ocelli five, arranged in semicircle just caudad of base of each antenna; dark area in connection with each group. One pair of setæ on epicranium near mid-dorsal line; a similar pair near mesal margins of ocelli groups; two strong setæ on each lateral surface of head near ocelli.

Thoracic segments very finely granulose. Cervical shield broad, black in color, strongly chitinized, smooth, widest at mid-dorsal region; margins regular, anterior margin very slightly conate, posterior margin slightly convex; covers greater part of dorsal surface of prothorax. Meso- and metathorax without traces of black, not strongly chitinized; color uniformly yellowish. Legs similar in size and color, each ending in a single, strong curved claw. Each thoracic segment with three pairs of well-developed setæ on lateral and dorso-lateral surfaces.

Cephalic margin of abdominal segments I–VIII bordered with black; IX–X devoid of dark color. Dorsal surface of VII and VIII darker than other segments. Posterior segments becoming narrower; IX narrow. Prolegs on III–VI and X. One pair of somewhat conical, fleshy projections on lateral aspects of each segment; one short, ventral seta and a longer, dorsal seta, latter about 0.27 mm. long, on each projection. Segment IX with four pairs of well-developed setæ on dorsal and lateral surfaces. Segment X with a pair of short setæ and one pair of longer setæ on dorsal surface; three setæ, two short and one longer, on each lateral surface; two setæ on caudal margin; and two very long setæ, 1.06 mm. in length, extending from the latero-caudal angles of posterior margin.

Second Instar.—This instar, as such, has not been described. Forbes ('10, p. 221), in his account of the life history of this species, states that "stage II" was "not seen; and no sign of leaf-mining was noticed." The same writer describes "stage

III", using an interrogation mark to indicate uncertainty, as
follows: "A transparent caterpillar, essentially like the full-
grown ones. The maximum number of gill-filaments is two, and
the anterior suprastigmatals and the last three pedals have but
one. Length about 4 mm.; head .6 mm." The writer has
reared larvæ through the early stages from eggs laid by females
in the aquaria and observed no indication of an instar between
the first and the one described below as the second, the latter
corresponding rather closely to the description of Forbes for
"Stage III. (?)".

A rather surprising change (Fig. 2) takes place at the first
ecdysis. The general shape of the larva is not changed but new
structures appear. Measurements show the body to be about
2.5 mm. long. It is almost transparent, and the color of the
material in the digestive tract shows through the body-wall,
giving combinations of yellow and green to the general color.

Head about 0.38 mm. wide, otherwise as in the first instar.
Thorax with margins of cervical shield black, remainder trans-
lucent; prothorax with five pairs of well-developed setæ; meso-
thorax with one pair lateral, filamentous gills; length of each
gill about equal to width of corresponding segment; metathorax
with two lateral, filamentous gills on each side, both of similar
length and resembling mesothoracic gills. Legs translucent.
Meso- and metathorax devoid of dark color. Abdomen without
dark markings; two lateral gill filaments on each side of all seg-
ments except last two, one filament with length about equal to
width of corresponding segment, the other about one-fourth
shorter; penultimate segment with one lateral, filamentous gill
on each side, about as long as width of segment; ultimate segment
devoid of gills. No gills on dorsal surface of body. Last two
segments with several pairs of setæ, one pair of which is terminal
in position, long, and stout. Otherwise similar to first instar.

The interesting part of the change from the first to the second
instar is the initial appearance of the tracheal gills in the latter.
In most of the specimens studied, the lateral gills were constant
in all respects, but a few showed variation from the typical
condition. One specimen showed a small, extra gill on the left
side of the ventral surface of the second abdominal segment.
Another specimen bore only one gill on the right side of abdom-
inal segments II, III, IV, and the left side of abdominal
segments II and VII.

Third Instar.—The conditions under which these larvæ must be reared make it very difficult to follow the ecdyses so that the exact number of instars can be determined. The following described instar is identified in this paper as the third since, in the examination of many specimens of different ages in the field and laboratory, no indication of an instar between it and the second could be found. Larval changes were also followed as accurately as possible in specimens reared from eggs and the same result was obtained. The writer believes that the results warrant the designation of this form of the caterpillar (Fig. 3) as the third instar.

Length, 4–5 mm. General color pale yellowish. Head about 0.44 mm. wide, otherwise very similar to second instar. Thorax with anterior margin of cervical shield dark, remainder translucent; five pairs of setæ on prothorax; mesothorax with one pair of lateral, filamentous gills and one pair of dorsal, filamentous gills; metathorax with three pairs of filamentous gills, one pair laterad, one pair dorsad, and another pair ventrad. First abdominal segment with three pairs of gills similar in shape and position to those of metathorax; segments II and III, with one pair of dorsal, two pairs of lateral, and one pair of ventral gills; abdominal segments IV and V with two pairs of lateral and one pair of dorsal gills; segments VI, VII, and VIII, with two pairs of lateral gills; segment IX with one pair of lateral gills; segment X devoid of gills; segments IX and X with several pairs of setæ, one of which is terminal in position and much longer than others.

It will be noticed that the above description agrees to some extent with that given by Forbes for "*Stage IV*", the chief difference being in the maximum number of gill filaments. Although the writer has never found an instar in which the maximum number of gill filaments was three, he is inclined to believe that the third instar of this paper is the same as "*Stage IV*" described by Forbes.

Later Instars.—Examination of a large series of caterpillars, varying from the third instar to the full-grown state, showed the existence of a number of types, based on gill characteristics, gradating from the former to the latter. Each successive type is characterized by increase over the preceding one in body size and in the number of gill filaments. Whether or not each type

represents an instar has not been determined and the discussion
of later instars will be left for a future paper. The full-grown
larva has been studied by Forbes ('10, p. 221) and the specimens
studied in this connection agree with his description in most
regards, assuming that his table of gill numbers represents an
average condition and not a constant one. The most striking
change in the later larval instars is the remarkable increase in
the number of gills. The maximum number of gills per segment
increases from two in the second instar to as many as ten per
segment in the full-grown larva. The total number of gills
increases from twenty-two in the second instar to one hundred
in the last one. The number of gill filaments per segment
increases from four in the second instar to as many as forty-eight
in the mature larva. The total number of gill filaments on the
whole body increases from forty to over four hundred. Such
a provision of tracheal gills would seem to be adequate for a
wide range of aquatic conditions.

Activities of the Larva.

Locomotion.—The young larvæ are active from the moment
of hatching, crawling restlessly about over the egg shells and
the adjacent leaf surface. Locomotion on the water-lily leaves
consists exclusively of crawling movements. In the younger
instars, particularly in the first, this method of locomotion is
slow, often appearing awkward and inefficient. Crawling, in
the older instars, is more active and vigorous and, under normal
conditions, constitutes a comparatively efficient form of loco-
motion. The efficiency of crawling as a method of locomotion
depends upon the character of the supporting surface. On
the yellow water-lily leaf, crawling is accomplished with some
degree of ease, except when the leaf, bearing larvæ on the upper
surface, is submerged, a condition which seems to require extra
effort. Crawling on the glass surfaces of the aquaria is very
slow and inefficient, consisting of little more than a mere clinging
to the glass, and change of position is accomplished with
difficulty. Other surfaces of a smooth, firm nature also afford
difficulties in crawling.

At no time during the larval period did the writer observe
any evidence of an ability to swim. In this connection, a num-
ber of experiments were tried with larvæ of all ages but results
were always negative. Random, writhing movements were

exhibited when larvæ were submerged apart from a supporting surface but such movements were ineffective so far as change of position was concerned. However, another form of locomotion will be described later in connection with the discussion of case-making which serves as a substitute for true swimming.

Case-making.—A very interesting phenomenon in connection with the life history of *N. maculalis* is the case-making activities of the larva. This habit is common to the genus *Nymphula*, both in foreign and native species. Of the latter, Packard ('84, p. 824) gave a brief account of case-making by what was apparently *N. icciusalis* Wlk. Hart ('95, pp. 167–172, 176–180) described it in *N. (Paraponyx) obscuralis* Grt. and *N. (Hydrocampa) obliteralis* Wlk. Forbes ('10, pp. 220–21) gave a brief description of case-making in *N. maculalis* Clem.

The observations of the writer confirm, in most respects, the brief description of Forbes on case-making in *N. maculalis*. However, a number of additional data have been secured and will be discussed in some detail. As mentioned above, the larvæ are active from the moment of hatching. They emerge from the eggs and wander about restlessly for a time before starting to feed. In some of the aquaria, this period of preliminary wandering lasted for two or three hours. In the laboratory, the young larvæ seemed to show a preference for the submerged lower side of the leaf on which they were reared. The young larva, under laboratory conditions, soon began to make an incision in the leaf which was extended in such a way that ultimately a portion of the leaf, oval or circular in form and about 2 mm. in maximum dimension, was cut out and drawn back on the lower surface of the yellow water-lily leaf so that the larva was enclosed. Sometimes the larva cuts out the upper surface of its compartment, thus making an independent case composed of two similar pieces of leaf tied together by silken threads.

As the larva increases in size, the cases are outgrown and new ones made. With the older larvæ, case-making is a simple and rather rapid process. In constructing a new case, the larva crawls to the lower surface of a leaf and usually begins work near the periphery so that the resulting piece is cut out of the edge. However, an occasional leaf is found in which the piece has been cut out near the midrib. Certain random, preliminary

movements are often performed, consisting chiefly of an apparent testing of the lower epidermis with the mandibles, before the larva settles down to the work of removing the piece. It works by using most of the length of the body as a radius and bending the anterior region as the incision is extended. After the initial incision is made, the head is held into the cut and a little to one side, thus placing the cutting plane of the mandibles at approximately right angles to the surfaces of the leaf. One-third of the complete incision may be made without changing the position of the posterior part of the body. Occasionally, a larva takes advantage of the overlapping margins of contiguous leaves. Since such a space is usually filled with water, the larva crawls into it, begins work, and in due time cuts an elliptical piece from one or both of the leaves.

The older larvæ utilize the excised pieces in making cases in several ways:

(1) A single piece may be cut out and tied flatwise against the lower side of the leaf.
(2) Two similar pieces may be cut out, forming a lens-shaped case, which is then tied flatwise to the leaf, or else becomes independent.
(3) Several pieces may be cut out, tied together into a case, and attached to the lower surface of the leaf.
(4) Two pieces may be cut out, tied together flatwise, and then attached endwise to the leaf.

The majority of the cases are placed on the lower, submerged surfaces of the floating leaves. Occasionally, cases containing larvæ are found on the dry, upper surfaces, a fact which suggests the possibility that the larvæ are not entirely dependent upon respiration by tracheal gills. It is a common thing to find numerous cases of various sizes attached to both surfaces of the submerged leaves of *Nymphæa americana*. How these larvæ get on the submerged leaves is not definitely known but it is possible that some of them, by wave action or other mechanical means, are dislodged from the floating leaves and sink to the submerged leaves, or else to the bottom from whence they crawl up the petioles to the leaves. The presence of young larvæ in such situations is discussed later.

The chief functions of the case appear to be (1) protection, and (2) support in the water. The protective function plays an important part in the life of the larva. These caterpillars occur in an environment where predaceous enemies are common and obviously the case is a rather efficient protection. The larva shows a very distinct tendency to respond to slight

mechanical stimuli by immediate retraction into the case, a
reaction which probably plays an important part in escaping
enemies.   Under normal conditions, the larva is apparently
very shy, never, according to the observations of the writer,
emerging completely from the case except in connection with
the construction of a new one.   At times, the anterior two-thirds
of the body is projected from the case but such periods of
partial emergence are of short duration, except when engaged in
a special form of locomotion to be described later.   Larvæ,
removed from their cases and placed in aquaria provided with
yellow water-lily leaves, very soon begin the construction of
a new case.

The second function of the case—that of support in the
water—is vitally connected with an interesting form of locomo-
tion.   The specific gravity of the older larvæ is greater than that
of water and, unless supported, they will sink.   The leaf tissue of
the yellow water-lily has a specific gravity distinctly less than
that of water and the oblong pieces cut out by the larva in
case-making are always buoyant enough to easily support it.
Therefore, all detached cases float at the surface and no effort
on the part of the larva is required to support itself in the
medium.   Where larvæ are numerous, individuals are often
found crawling over the top of the water-lily leaf, carrying the
cases with them.   To accomplish this form of locomotion, the
larva extends the anterior part of the body from the case, uses
the true legs as locomotor organs, and holds the case with the
prolegs.   When detached cases are dropped in the water, the
larva performs certain movements which result in a change of
position in space.   As mentioned before, no evidence of an ability
to swim was observed when larvæ were isolated from their cases.
However, they do possess a form of locomotion in water in con-
junction with their cases.   The anterior portion of the body is
projected from the case into the water and vigorous, horizontal,
side to side motions are executed which result in the propulsion
of both larva and case.   It does not constitute a very efficient
form of locomotion but is effective enough to bring the larva in
contact with other water-lily leaves.   If the horizontal move-
ments are equal on either side of the long axis of the body, the
result is a backward movement approximately in a straight
line.   If, as is often the case, the strokes are stronger on one
side than the other, the result is an irregular rotation.

The effect of case-making upon the food plant is frequently serious. Some of the yellow water-lily beds (*N. americana*) about Douglas Lake are heavily infested at times with the larvæ of *N. maculalis* and suffer greatly (Figs. 12–19). The total effect of the larvæ on the food plant includes the amount of plant tissue consumed as food and the plant tissue utilized in case construction. According to the observations of the writer, the plant suffers much more from the case-making than from the removal of tissue for food. Case construction results in a reduction of the leaf surface which may be extensive enough to leave only the midrib. The writer observed beds of *N. americana*, in August, which, as nearly as could be estimated, had lost 40 per cent. of the total leaf surface by the case-making activities of these larvæ.

Food.—Very young larvæ, reared in shallow aquaria, fed on the lower side of the yellow water-lily leaf, feeding and case-making being accomplished at the same time. The translucency of the body made it possible to observe the first occurrence of green plant tissue in the digestive tract. After the case was made, the tiny larva fed to some extent upon the tissue of the case. However, the normal field habits of the larva in the first instar were not determined. In rearing young larvæ in aquaria, some difficulty was experienced in securing the second instar and in preventing a very high mortality among those which hatched from egg masses. The following circumstantial evidence suggests that possibly the larvæ, after hatching, settle to the bottom and after one or two ecdyses, approach the surface of the water on the petioles of the water-lily:

(1) Recently hatched larvæ have a tendency, in the aquaria, to drop to the bottom and to wander about.
(2) The first and second instars were not found on the floating leaves of the yellow water-lily where the egg masses occurred.
(3) It was frequently observed that in water-lily beds in which the floating leaves had petioles two or more feet long, the *submerged* leaves bore young larvæ (third instar or a little later) while the floating leaves bore only the more advanced larvæ. Some of the submerged leaves had petioles only about one inch long, so that the leaf was practically on the bottom.
(4) Very rarely did pupæ occur on the submerged leaves.

Larvæ, hatching in very shallow aquaria, ate the yellow water-lily leaf tissue and some developed into the second instar, but it is possible that it was not the normal reaction and that the first instar may be passed on the bottom. In later instars,

feeding was confined largely to adjacent leaf tissue not a part of the case itself. All excrement was voided outside of the case, thus providing for the cleanliness of the interior.

Forbes ('10, p. 220) states that in addition to *Nymphæa*, *Castalia* and *Brasenia* are used by *N. maculalis* in case-making and his description leads one to infer that all of these plants are used as food. The writer has found no evidence of feeding or case construction involving plants other than *N. americana* although *Nymphæa* and *Castalia* intermingle in the same beds. *Brasenia* does not occur in the Douglas Lake region.

Respiration.—Respiration in the first instar is apparently cutaneous. Tracheal gills have not yet appeared and, since the larva is almost constantly submerged, it would appear that it must of necessity utilize the dissolved oxygen of the water by absorption through the body-wall. Larvæ, hatched and reared in the laboratory, almost invariably sought the lower side of the water-lily leaf regardless of whether the leaf was submerged or floating. A study of the various situations in which the larvæ of *N. maculalis* occurred most abundantly showed that the water contained a considerable amount of dissolved oxygen, due to the exposure to the air and the agitation by wind and wave action. It is possible that the oxygen demands of the larva in the first instar are low enough that they can be satisfied by the cutaneous form of respiration and special organs are not demanded.

After the first ecdysis, tracheal gills appear, each gill containing a primary branch from the longitudinal tracheal trunks. The appearance of about fifty gill filaments in the second instar would seem to be ample provision for the increased oxygen demand. The marked increase in the number of gills and in the number of branches of each gill in the later instars has been discussed.

The occasional appearance of larvæ on the upper surface of the leaf seems to indicate an ability to pass at least a limited time out of water. Instances of pupation on the upper surface of the leaf were observed in the field and the time required for a larva to emerge from the water, locate the case, and construct the silken inner covering would seem longer than the individual could survive without some form of oxygen supply. No data were secured on the mode of respiration under these conditions.

Possibly, cutaneous respiration continues to be operative in the later instars.

Dissemination.—The larvæ have several methods of dispersal:

(1) Since *N. americana* grows in beds in which the leaves are very frequently contiguous or overlapping, the larvæ hatching from a single egg mass may, by crawling, scatter over a number of leaves. The older larvæ are more efficient at crawling and may ultimately get a considerable distance from the original food plant.

(2) Larvæ may propel themselves in detached cases from one food plant to another as already described.

(3) Wind, wave action, and currents are sometimes very effective in scattering detached cases containing larvæ.

(4) Water-lily leaves, broken from the petioles by wave action or loosened by the attacks of certain species of insects, frequently bear the attached cases of *N. maculalis* and such leaves float about from place to place at the will of the waves and currents. This form of dispersal was very common in some of the water-lily beds about Douglas Lake, where the plants were badly affected by the larvæ of *Hydromyza confluens* (Welch, '14a, pp. 139-140) which cause the petiole to break under very slight side to side strains, and by the larvæ of *Bellura melanopyga* (Welch, '14b, p. 104) which sometimes sever the leaf from the petiole near the upper end of the latter.

PUPA (Pl. VIII, Figs. 6–7).

Forbes ('10, p. 222) gives the following brief description of the pupa: "*Pupa* similar in general form to that of obscuralis, as described by Dyar, but of the seven ridges near the tip of the abdomen beneath, only the central one remains, and the anal opening is not distinctly Y-shaped. The case for the hind legs varies considerably in length." Measurements of a large number of pupæ showed that there is some variation in size. The length, exclusive of the spike-like setæ on the vertex, varies from 10 mm. to 14.5 mm., average 12.6 mm. The maximum diameter is in the region of the second to the fourth abdominal segments and, in the specimens examined, the average is 3.4 mm., the extremes being 2.0 mm. and 4.0 mm. The color is uniformly light yellow, except in specimens about ready to transform in which the developing colors of the adult begin to show through the pupal integument. Pupæ preserved in alcohol lose the yellowish appearance and become whitish. The body is rather soft, smooth throughout, naked, and semi-opaque. The anterior region tapers slightly cephalad while the posterior region tapers distinctly caudad. The abdomen is bent so that the ventral surface of the body is nearly plane while the dorsal surface is distinctly convex.

The head is smaller than the prothorax. It bears on the vertex two slender, porrect, very slightly dehiscent setæ, reddish brown in color, and approximately 0.21 mm. in length. In the older pupæ, the eyes are dark in color and show through the integument. The antennal cases lie parallel to the second leg cases, extending with the latter around on the ventral surface of the body and approaching the mid-ventral line. In the specimens examined, the length of these antennal cases varied, depending, apparently, upon the age of the pupa. The extent of the variation is from a position opposite the first pair of abdominal spiracles to the posterior tips of the wing cases. They acquire an external segmentation corresponding to the segmentation of the antennæ within and have a distinctly moniliform appearance. From the ventral surface of the head, a long, tapering, double sheath extends caudad along the mid-ventral line of the body to a point approximately opposite the tips of the wing cases. It contains in its cephalic end the developing palpi and proboscis.

The thoracic segments and their associated parts are similar in color and appearance in the newly transformed pupæ. On the ventral surface, the cases for the wings and legs cover the greater part of the first four abdominal segments. The tips of the wing cases extend almost to the caudal margin of the fourth abdominal segment. The ventral sheath, for the hind legs, is prolonged caudad almost to the tip of the abdomen. As stated by Forbes ('10, p. 222), the length of this ventral sheath varies considerably. In the large number of pupæ examined by the writer, the caudal extremity varies in position from the caudal margin of the sixth abdominal segment to the posterior end of the body, a variation represented in extent by the combined width of the three posterior segments of the abdomen. The sheath for the second pair of legs also varies in length. It often extends but little if any beyond the tips of the wing cases, but specimens have been studied in which it extended to the caudal margin of the fifth abdominal segment. The case for the first pair of legs is shorter than the others, the posterior extremity usually reaching a point opposite the spiracles on the third abdominal segment, although this case is likewise subject to some variation in length. Observations on pupæ of different ages lead the writer to believe that the length of the leg cases is

dependent, to some extent at least, upon the degree of develop-
ment of the quiescent stage, the length increasing as the time
of emergence of the adult approaches. All of the appendages of
the head and thorax become more and more apparent and it is
often possible to pick out the female pupæ by the uniform dark
slaty gray appearance of the front wings. The leg cases become
increasingly distinct and acquire an external segmentation
corresponding to that of the enclosed leg.

The abdomen is widest at its junction with the thorax and
tapers gradually caudad. Except at the extreme posterior end
of the body, the intersegmental grooves are broad and well-
defined. The second, third, and fourth abdominal segments
bear each a pair of large, lateral, conspicuous spiracles, all of
nearly uniform size, and borne on fleshy, conical tubercles. The
slit-like opening is transverse in position and surrounded by an
almost circular, dark orange, chitinized peritreme. Separated
from the peritreme by a narrow space and at a slightly lower
level is a fine, brown, concentric line. The various structural
elements of these spiracles vary in size in the different specimens
and to a limited extent in the same specimen. The average
dimensions of the peritreme are about 0.232 x 0.264 mm., the
average length of the slit-like opening is approximately 0.14
mm., and the average diameter of the outer ring is about 0.28
mm. Vestigial spiracles occur on abdominal segments V–VII
but are so inconspicuous that close examination under mag-
nification is usually required to locate them. The ventral sur-
face of the tip of the abdomen bears a number of short, longi-
tudinal carinæ, arranged in two groups. The intersegmental
grooves in this region are obscure and careful examination is
required to determine the segmental position of these groups
of carinæ. The anterior group occurs on the eighth abdominal
segment and usually consists of a single, median carina or a
pair of similar carinæ, one on either side of the median line.
The second group of carinæ occurs near the anterior margin of
the ninth abdominal segment and consists of a single, median
carina separating the components of a pair of similar carinæ.
Sometimes a second pair of lateral carinæ are also present. The
crests of the carinæ in both groups are brownish in color while
the sides have the same color as the adjacent parts of the
abdomen.

The number and arrangement of these carinæ on the ventral surface of the ninth abdominal segment present considerable variation. Forbes ('10, p. 222) states that this pupa is similar in general form to that of *N. obscuralis* "but of the seven ridges near the tip of the abdomen beneath, only the central one remains". The writer has examined a large number of these pupæ during the past five summers and has failed to find a single pupa which possessed only the single, median carina. The first pair of lateral carinæ is always present in addition to the median one and, as stated above, there is sometimes present a second pair laterad of the first. When a second pair is present, the component carinæ are usually smaller than the other carinæ and not so readily distinguished. In *N. obscuralis*, as described by Hart ('95, p. 173), the first group of elevations are described as follows: "Apex of abdomen subacute; ninth segment beneath with a faint elevated line at middle, and a small elevation each side." In the figure accompanying this description, the "small elevation each side" is represented as circular in contour. This condition seems distinctly different from that existing in *N. maculalis* since, in all of the pupæ examined, the single elevated line, when present, is unaccompanied by conical elevations of any sort, and when absent, it is represented by a pair of similar, longitudinal elevations. Furthermore, this group of elevations is on the eighth abdominal segment. The above description probably does not include all of the variations which exist since the writer found one specimen in which the anterior group of carinæ consists of three pairs of elevations, diminishing in size on either side.

Caudad of the second group of carinæ is a distinct Y-shaped impression. Forbes ('10, p. 222) makes the following statement: " . . . . . and the anal opening is not distinctly Y-shaped." All of the specimens examined in this connection show this ventral impression to be of such structure that the expression "Y-shaped" describes it quite well.

As already stated, the full-grown larva usually attaches its case to the lower, submerged surface of a water-lily leaf and transforms into the pupa. Just before pupation, a dense, whitish, apparently complete, silken covering is spun around the larva. This silken covering adheres closely to the inner walls of the case and is strongly attached at the periphery. It is

elliptical in outline, the dimensions usually being about 1.25 x 2 cm. The maximum thickness is usually but little more than the maximum diameter of the pupa. This silken covering is relatively strong and not easily torn open.

The case varies to some extent in size and shape. In general, it is elliptical and has dimensions varying from 1.5 x 2 cm. to 2.5 x 5 cm. The vast majority of the pupal cases are attached to the lower surface of the floating water-lily leaves and are thus constantly submerged. Pupal cases have been found on the upper surface of floating water-lily leaves, a position which minimizes contact with the water. The fate of such pupæ is not known. A few pupal cases have also been found on the submerged water-lily leaves, several inches under the surface of the water.

The external surface of pupæ is not easily wetted and they float if removed from the silken coverings and placed in water. The fate of pupæ which accidentally become removed from their cases is not known. It is said (Miall, '95, p. 233) that the pupæ of certain European species of *Nymphula*, when removed from their silken coverings and placed in water, live for a time but do not transform into adults.

Dissemination.—In connection with the discussion of the dissemination of the larvæ, mention was made of the fact that an indirect method of distribution occurs, due to the influence of wind and waves, or the work of other insects, or both. The pupæ are sometimes scattered in the same way. The work of the larvæ of *Hydromyza confluens*, *Bellura melanopyga*, and others, frequently bring about the separation of the leaf or portions of the leaf from the petiole, permitting them to float about at random. Such detached leaves often bear pupal cases of *N. maculalis* and may be carried some distance from the original breeding place. After storms in which portions of the floating water-lily leaves are torn away by wave action, pupæ are sometimes found on the opposite shore.

THE ADULT.

Adults of *N. maculalis* have been taken about Douglas Lake by the writer from June 28 to August 30 but these limits are probably too narrow. They are normally confined to the region surrounding the food plants of the larva and the few scattering adults which are sometimes found remote from yellow water-

lilies are probably individuals which have emerged from pupæ which have been drifted away from the original breeding place by the wind and waves, rather than individuals which have voluntarily wandered from the place of emergence.

The adults of *N. maculalis* are largely nocturnal in habit. Occasionally, individuals may be observed in flight during the day but, in general, the period of activity begins shortly after dusk. During the day, they can usually be driven to flight by walking through the water-lilies or in the vegetation growing near the edge of the water, or by beating the undergrowth fringing the beach near the water-lily zone. On calm, clear days, adults are commonly found at rest upon the upper surface of the water-lily leaves, but on windy days they usually seek the undergrowth near the edge of the beach. They respond readily to slight disturbances by short flights but observations both in the field and in the aquarium lead the writer to believe that voluntary flight during the day is not common. Females in the breeding cages remain inactive throughout the entire day. Diurnal flight is apparently at random and the selection of objects of support a matter of chance. Only one constant feature was observed, namely, adults never made long flights away from the immediate vicinity of the water-lily beds. Individuals, driven from resting positions, often flew over the open water, never rising high above the surface, dropping momentarily on the surface from time to time, but almost invariably, after a flight of three or four rods, returning to the same vicinity. Individuals which happened to fly out from shore during a strong wind had difficulty in returning and were frequently carried far out on the lake.

The adult apparently suffers little if any from contact with water. The usual position of the pupa is such that, on emergence, the adult is, of necessity, compelled to come to the surface through a certain depth of water. Individuals flying over open water, as described above, frequently drop momentarily on the surface, taking wing again without difficulty. Individuals, whose powers of flight have been exhausted, drop ultimately to the surface and may rest there for a considerable length of time.

Nothing was discovered concerning the feeding habits of the adult. Individuals have lived for days in an aquarium without food but the possession of well-developed mouth parts points rather definitely to a feeding habit.

Only incidental observations on the enemies of this species were made in this connection. It is probable that the possession of a case in the larval and pupal stages is a provision whereby considerable protection is afforded. The larvæ occur in situations which are rich in predaceous animals of several kinds and there is no reason to suppose that such fleshy larvæ would be exempt from attack. One of the robber-flies, common in the Douglas Lake region, preys on the adult and specimens of the latter have been taken with adult *N. maculalis* in their claws. Although this robber-fly is a vigorous enemy, it seems probable that the nocturnal habit of the moth prevents greater fatality from this enemy.

Nymphula icciusalis Walker.

Early Stages.

Nymphula icciusalis is abundant on the north shore of Douglas Lake about the bays, beach pools, and inlets, all of which contain quantities of *Potamogeton, Vallisneria,* and other aquatic plants. By confining females in aquaria containing the leaves of several aquatic plants, egg masses were easily secured and the process of hatching and the early development of the larva were observed. Since the early stages of the life history have not been described, the following data have been included in this paper. Packard ('84, p. 824) figured a larva, which he supposed to be *N. icciusalis.* Forbes ('10, pp. 225–6) reared a single larva through to maturity and reported close correspondence of data with those of Packard, but made no mention of the eggs or early larval instars. Miller ('12, pp. 127–134, 245) made some observations on this species, described some of the activities of the larvæ, made slight mention of the pupa and of the eggs, and described the full grown larva in considerable detail.

THE EGG.

Place and Method of Deposition.—The following data were taken from egg masses deposited by females in the aquaria and from numerous egg masses taken in the field. Egg masses from both sources were laid on the leaves of *Potamogeton natans.* In aquaria containing only *Nymphæa americana,* females, after some delay, deposited eggs on the leaves of this plant in the characteristic way but this was evidently not a normal reaction.

Eggs are laid in a definite cluster on the lower surface of the leaf and very near the margin. No egg masses were found in ·connection with punctures or artificial breaks through the leaves. The eggs are arranged in concentric rows, usually four, which are separated by uniform spaces, each row being curved ·so that the concave side is always towards the margin of the leaf. The number of eggs composing the clusters examined in this connection varies from 17 to 76. Clusters are sometimes placed so closely together that they appear to be almost confluent. The row of eggs nearest the margin of the leaf is always at least 2 mm. from the edge and sometimes as much as 5 mm. Oviposition was not observed but the position of the egg mass and the distance of the rows from the edge of the leaf indicate that possibly the female lays the eggs, in a manner similar to that suggested for *N. maculalis*, by clinging to the edge of the leaf, extending the ovipositor under the edge and swinging it around, thus depositing the eggs in concentric rows.

Description.—The eggs are elliptical in outline, slightly flattened, smooth, uniform in size, and 0.45 mm. x 0.6 mm. in dimensions. They are whitish in color, being distinctly lighter than the leaf surface on which they are placed. When first laid, they show no external signs of internal differentiation.

Development.—The egg period is from ten to eleven days. Eggs, deposited in the aquaria, develop in the same way and at the same rate as the egg masses collected in the field. During the first two days subsequent to oviposition, no internal changes are evident. At the end of about fifty hours, the eggs begin to show signs of internal differentiation and, during the following 24–36 hours, a dark band develops within, similar in some respects to the one which appears in the early development of the eggs of *N. maculalis*. This band has a shape somewhat like the letter J and is constant in its position in all of the eggs, the more curved end of the band being invariably in the end of the egg remote from the edge of the supporting leaf. After five days of development, the dark band has increased considerably in size and has changed somewhat in shape, showing distinct differences in the two ends, one being larger and more blunt and recognizable as the future head of the caterpillar. During the seventh to the ninth day, the black areas on either side of the head appear and the longitudinal tracheæ are visible. The

tips of the mandibles are also turning brown. At the end of the ninth or the beginning of the tenth day, the outlines of the complete caterpillar are visible through the egg capsule. It is coiled upon itself, the caudal end reflected around the head, and the dorsal surface usually turned from the surface of the leaf. The dark, chitinized head capsule and prothoracic shield are the most conspicuous parts. The intersegmental grooves are visible to a slight degree. The abdomen and the two posterior segments of the thorax are devoid of dark color or markings. At this stage, the mandibles are observed to be in active motion and contractions of the body preliminary to hatching are evident.

The Larva (Pl. VIII, Fig. 11).

First Instar.—Larva small; length about 1.4 mm.; maximum diameter of head 0.25 mm. Body whitish; translucent; head and prothoracic shield very dark-brown and heavily chitinized; remainder of body devoid of dark color and quite flexible. No tracheal gills. Principal setæ as in figure 11. Anal setæ 0.14 mm. long. Dorsal surface of segments often showing transverse folds and wrinkles. Prolegs with hooks arranged in transverse ellipse; usually 22–24 hooks on each body proleg; about 7–9 hooks on anal prolegs.

Case-making.—Small, elliptical cases, 2.5–3 mm. long, are constructed soon after hatching. They may be attached or independent and the leaf material may be cut from the periphery or from the middle of the leaf. The young larvæ show a very distinct tendency to remain on the lower sides of the leaves where all of the work of excising pieces of leaves is done. Cases are outgrown and new ones constructed, much as has been described for *N. maculalis*, and they seem to serve similar functions. Attached cases usually occur on the lower side of the supporting leaf.

Food.—Packard ('84, p. 825) found his supposed larva of *N. icciusalis* making cases from the leaves of *Menyanthes trifoliata*. Forbes ('10, p. 226) reported his specimens on *Potamogeton* and states that they would not eat *Limnanthemum*. Miller ('12, pp. 127, 130) found caterpillars feeding on *Potamogeton natans* and states that they may also work on *Marsilia quadrifolia*. The egg masses, larvæ, and pupæ occur predominantly on *Potamogeton natans* in the Douglas Lake region,

although a few larval cases were found, in part, composed of fragments of leaves of *Vallisneria*, a fact which suggests that this plant may be used for food. No evidence of feeding on any of the water-lilies was observed. The larvæ are active from the moment of hatching and soon begin feeding, evidence of which is the early appearance of yellowish matter in the digestive tract.

SUMMARY.

Aquatic Lepidoptera are very limited in number and the American species are little known. They rival other aquatic insects in the character of their unique habits and adaptations. Two species are considered in this paper.

I. *Nymphula maculalis* Clem.

1. Eggs are deposited only on the lower, submerged surface of the leaves of the yellow water-lily, *Nymphæa americana*, in masses arranged in concentric rows.

2. Egg masses, in the Douglas Lake region, are invariably placed about the egg holes of the chrysomelid beetle, *Donacia*.

3. Laboratory observations and experiments on females in aquaria yielded the following data: (a) Eggs were invariably deposited at night. (b) Eggs were invariably placed about *Donacia* egg holes when the latter were available. (c) Oviposition may extend over five successive nights. (d) One female may use several *Donacia* egg holes before oviposition ceases. (e) Maximum number of eggs laid by a single female was 617. (f) In the absence of *Donacia* egg holes or other similar punctures in the water-lily leaves, oviposition was usually delayed but ultimately resulted in the deposition of small egg masses on the lower side of the leaves at the margins. Egg masses were deposited about artificial punctures and incisions of various sizes and shapes, the dimensions of which apparently had little to do with the selections.

4. The egg period is about eleven days. There is a definite and constant orientation of the eggs in the mass since the heads of the larvæ invariably develop in the ends of the eggs nearest the leaf puncture.

5. The larva in the first instar is devoid of tracheal gills and respiration is apparently cutaneous.

6. Tracheal gills first appear in the second instar. Paired, lateral, filamentous gills occur on all of the segments except the prothorax and the last abdominal. Maximum number of gills per segment is two.

7. In the third instar, an increase in the number of gills appears, the maximum number being three. Dorsal, paired, filamentous gills also appear.

8. The sole method of locomotion by larvæ is an inefficient crawling. There is no evidence of an ability to swim. When supported by a case, change of position can be effected by side to side motions of a portion of the body extended into the water.

9. Case-making is a constant larval activity from time of hatching to pupation and sometimes seriously reduces the leaf surface of the food plants. The chief functions of the case seem to be (1) protection, and (2) support in the water.

10. No evidence of feeding or case construction which involved plants other than *Nymphæa americana* was observed, although the larva has been reported in connection with *Castalia* and *Brasenia.*

11. After the first instar, tracheal gills constitute the larval respiratory organs. The maximum number of gills increases with advancing age from two per segment in the second instar to as many as ten per segment in the mature larva. The total number of gills increases from twenty-two in the second instar to one hundred in the mature larva. The number of gill filaments per segment increases from four in the second instar to as high as forty-eight in the full-grown larva. The total number of gill filaments on the body of a larva increases from forty in the second instar to over four hundred in the full-grown larva.

12. Dissemination in the larval stage is accomplished by crawling over contiguous leaves; by voluntary propulsion in detached cases; by the effects of winds, waves, and currents on detached cases; and indirectly by the work of certain other insects which cause a separation of the leaves of the food plant from the petiole.

13. The pupa is described in detail. It is usually attached to the lower, submerged surface of the water-lily leaf and is enclosed in a silken covering which, in turn, is surrounded by the last larval case.

14.   Pupæ are disseminated by indirect methods. Winds and waves, assisted by the work of certain insects, may scatter pupal cases widely.

15.   The adult moth is largely nocturnal in habit. It suffers little, if any, from contact with the water, and in extended flights over water may drop to the surface for short rests.

II.   *Nymphula icciusalis* Wlk.

16.   Eggs are deposited on *Potamogeton natans*. In the aquaria, females, in the absence of *Potamogeton*, deposited eggs, after some delay, on *Nymphæa americana*.

17.   Oviposition is independent of the activities of other animals.

18.   Development of the egg requires ten or eleven days. As in *N. maculalis*, there is a definite and constant orientation of the egg, when deposited normally, since the head of the larva always develops in the end nearest the edge of the leaf.

19.   The first instar is described for the first time.

20.   Case-making, similar to that of *N. maculalis*, is a normal activity of this larva. The great majority of the cases studied were made from leaves of *Potamogeton natans* but a few were composed, in part, of fragments of leaves of *Vallisneria* which possibly is another food plant.

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EXPLANATION OF PLATES.

PLATE VII.

Figs. 1-10. *Nymphula maculalis.*
Fig. 1.   Dorsal view of recently hatched larva.
Fig. 2.   Dorsal view of larva in the second instar.
Fig. 3.   Dorsal view of larva in the third instar.
Fig. 4.   Egg as it appears immediately before hatching.
Fig. 5.   Egg masses on lower surface of leaf of *Nymphæa americana. p,* puncture
            through leaf made by female *Donacia; d,* eggs of *Donacia* sp.; *n,* eggs of
   *Nymphula maculalis.*

PLATE VIII.

Fig. 6.   Ventral view of pupa.
Fig. 7.   Lateral view of pupa.
Figs. 8-10. Ventral view of terminal segments of pupa, showing some common
            forms of variation in number and arrangement of carinæ.
Fig. 11.   Dorsal view of larva of *Nymphula iccinsalis.*

PLATE IX.

Figs. 12-19. Leaves of *Nymphæa americana* showing characteristic work of larvæ
            of *Nymphula maculalis.* Figs. 12, 13, 14 and 17 show extent to which
            surface of food plant may be reduced. In Figs. 13, 16 and 19, the small
            marginal incisions are the work of young larvæ. In Figs. 12, 14 and
            17, the broad marginal incisions were produced by full-grown larvæ.

P. S. Welch.
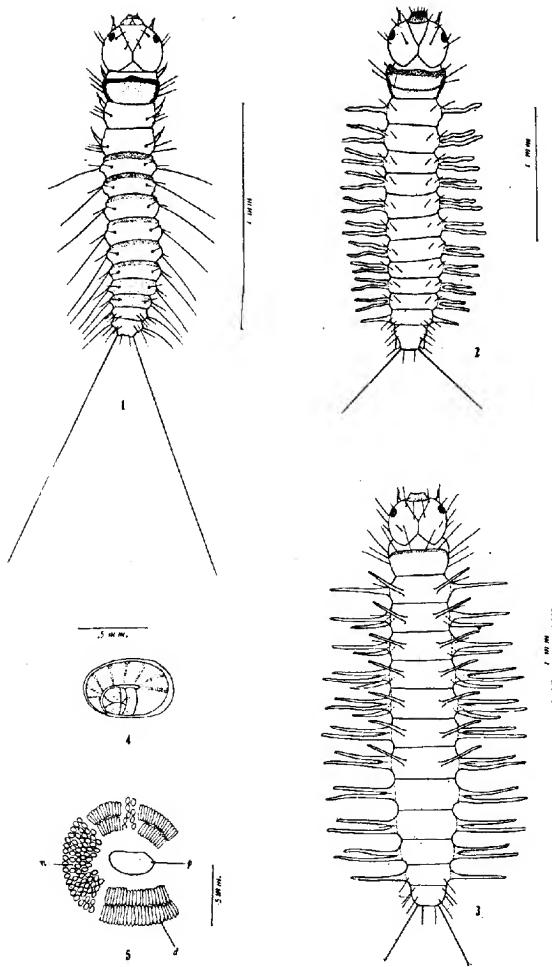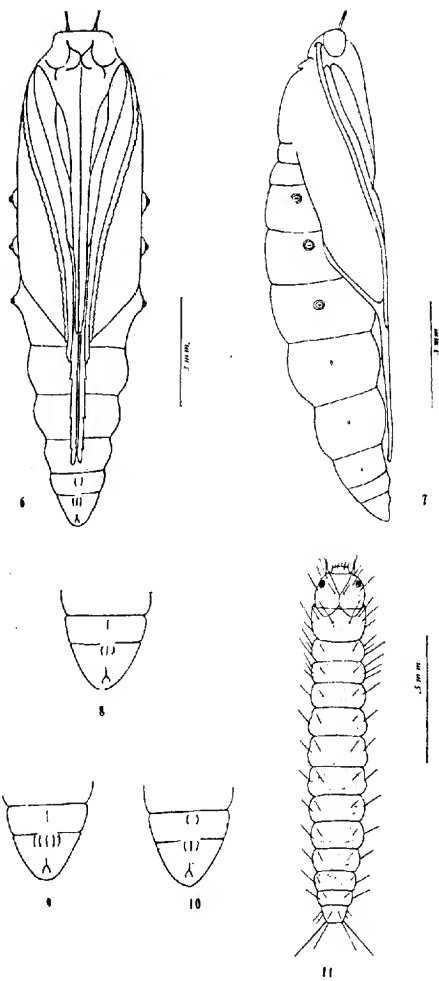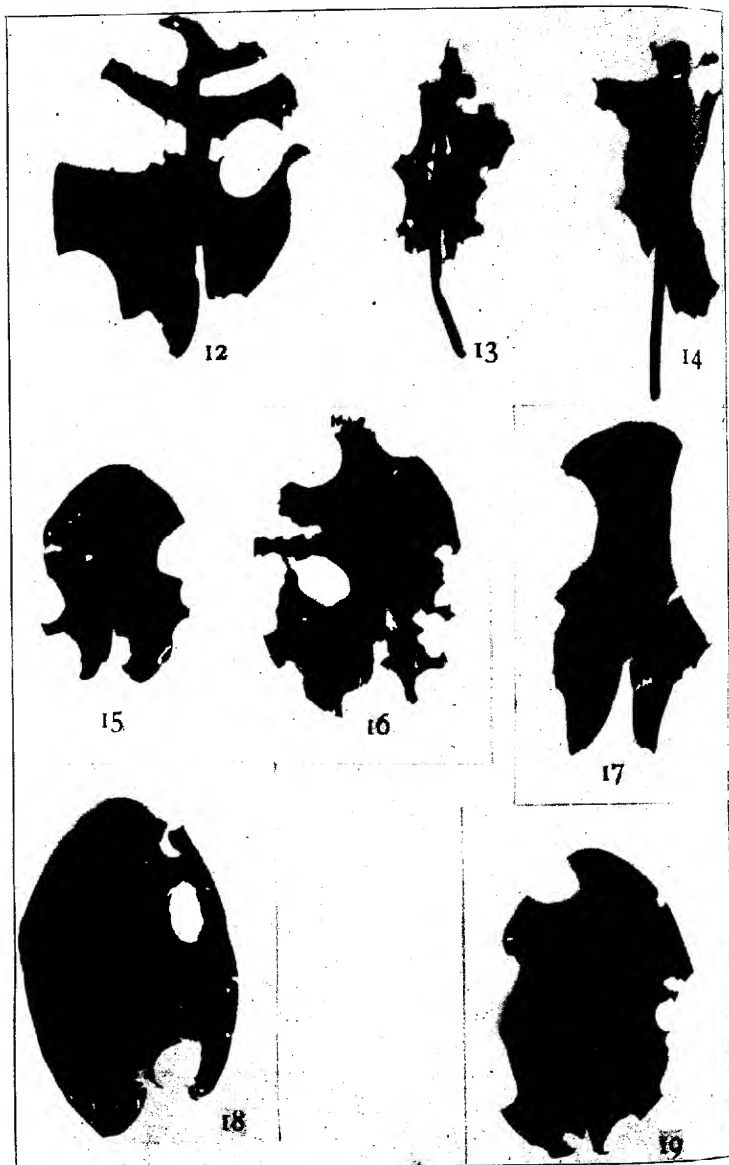
SYNOPSES OF ZODION AND MYOPA WITH NOTES ON OTHER CONOPIDÆ.

NATHAN BANKS.

For several years I have been accumulating material in this family, and the occasion of determining some western material induces me to publish descriptions of certain new species and to tabulate two of the genera, *Myopa* and *Zodion*, although the table of the latter genus is rather unsatisfactory.

These insects, like most parasitic ones, are variable in size; thus our two Eastern Occemyias cannot be separated by size as has been stated, each of them having large and small specimens. In the Myopinæ several species are widely spread, thus *Myopa vesiculosa* and *Zodion fulvifrons* occur in California as well as the East, and *Myopa pilosa* which was described from California is probably the same as our Eastern *M. vicaria;* also *Zodion pygmæum* from California and Nebraska seems to agree with our Eastern *Z. nanellum, Myopa clausa* I have from Utah, and *Zodion perlongum* and *Z. parvum* described from New Mexico and Arizona occur here in Virginia. *Z. obliquefasciatum* is also widely distributed, and *Occemyia loraria* occurs in Oregon as well as the East. In the Conopinæ, the species are more local, and the Western and Southwestern species are different from the Eastern ones; the Western species usually with more yellow upon them.

Conops arizonicus n. sp.

Face whitish, cheeks wholly pale, front and vertex dark rich brown, except that the white extends up as a narrow silvery stripe on inner orbits, and the dark extends down a little on the facial ridges. Antennæ dark brown, the third joint fully one and one-half times as long as the second; thorax and abdomen black, shining; last segment of abdomen more grayish pollinose and transversely wrinkled; hypopygium mostly shining black; legs blackish, extreme tips of the femora and basal half or third of tibiæ pale. Vertex, thorax, abdomen and legs with short blackish hair; wings with large costal dark cloud to end of second vein, extending directly downward to tip of the fifth vein; extreme tip dark. These marks are like those of *C. sylvosus*, except that here the cloud extends unbroken to the fifth vein and the abdomen does not show pale bands; halters pale. The ventral plate is not as large as in *C. sylvosus.*

Length, 7 mm.

From Palmerlee, Ariz., Aug. (Biederman). It is distinguished from *C. sylvosus* by the much longer third joint of antennæ, and the second joint not quite as long as in that species.

Conops brachyrhynchus var. semifuscus n. var.

Agrees with the type in structure and general coloration. The femora are almost wholly pale; the pale mark on tip of second and base of third abdominal segment is much longer, the last segment and basal part of hypopygium more yellow; the humeri yellow pollinose and the dark of wings stops at the third vein (in *C. brachyrhynchus* the dark gradually fades off.).

From Jemez Springs, N. Mex., 6 July (Woodgate).

Zodion.

In this genus are a number of closely related species; several of the Eastern forms are best separated by the shape of the ventral plate of the female. The forms intermediate in size I have placed twice in the following table, since they vary in size. *Z. fulvifrons* sometimes has the first posterior cell closed, so it also occurs twice in the table.

1. Thorax and abdomen gray, with very distinct black spots; legs pale, also with black spots...*pictulum*
   Thorax, abdomen and legs with only indistinct black spots or with lines or streaks..2
2. Thorax with two pale submedian stripes, abdomen largely pale, with oblique dark bands...*obliquefasciatum*
   Thorax without pale stripes...3
3. Palpi rather long, clavate...*palpalis*
   Palpi minute, cylindric..4
4. Very small species, hardly over four millimeters........................5
   Larger species, nearly six or more millimeters in length................9
5. Last joint of antennæ wholly pale; first posterior cell closed..........6
   Last joint of antennæ wholly pale; cell open; legs black, abdomen not marked with pale...*triste*
   Last joint of antennæ dark at tip......................................7
6. Cell petiolate; abdomen of ♂ mostly dark............................*parvum*
   Cell closed in margin; abdomen of ♂ mostly pale...............*abdominale*
7. Cell short petiolate; basal part of ♂ abdomen pale yellowish........*scapulare*
   Abdomen black with gray marks; cell open...............................8
8. Eastern specimens..*navellum*
   Western specimens (probably the same)..........................*pygmæum*
9. First posterior cell closed...10
   First posterior cell open..12
10. Abdomen of ♂ pale yellowish at base; last joint of antennæ dark at tip.
    scapulare
    Abdomen not paler at base; last joint of antennæ not dark at tip..........11
11. Thorax gray with two or three dark stripes; abdomen not usually pale.
    fulvifrons
    Thorax not so plainly marked, abdomen of ♂ pale yellowish.....*abdominale*

Zodion fulvifrons Say.

Say says that the thorax has two distant brown lines. This plainly agrees only with *Z. abitus* Adams; the first posterior cell varies from open to closed. I have therefore no hesitation in considering *Z. abitus* a synonym of the true *Z. fulvifrons*. *Z. rufifrons* Macq. was from Philadelphia. He says the thorax with "nuance de cendre argente" which will apply far better to *Z. fulvifrons* than to any other Eastern species. The rest of his description will fit any of our Eastern species. *Z. fulvifrons* has the ventral plate low, and much broader than long.

Zodion perlongum Coq.

Described from the West, it occurs here in Virginia. The long, compressed abdomen, and the very long ventral plate will distinguish the female. What I believe is the male has a rather pale abdomen. Mr. Greene has taken it at Broomall, Pa. Most of the specimens are taken in September.

Zodion intermedium n. sp.

Face whitish, antennæ reddish, front fulvous, in some specimens much darkened on the vertex and the dark reaching forward in a forked stripe; thorax above brown, with four black stripes, the intermediate pair only in front, the sublateral pair not extending forward, lateral spots, and transverse suture often black; metanotum dull black. Abdomen black, yellowish gray pollinose, especially on sides and a middle stripe; legs pale, femora dark above, last tarsal joint black; wings rather yellowish on base, veins beyond base dark. Vertex, thorax, abdomen and legs clothed with black hairs. Proboscis beyond palpi about one and one-half times as long as head-height. Ventral

plate of female about one and one-half times as long as broad, narrowed toward tip, behind at tip the dark striated area is very narrow. Posterior cell open.

Length 7.5 mm.

From Pocono Lake, Pa., and Clementon, N. J. May and July, all from Mr. C. W. Greene. Cotypes in his and author's collection.

Zodion sayi n. sp.

Very similar to *Z. intermedium*, but smaller. Face, front, antennæ, thorax, abdomen and legs colored and marked as in that species. The wings also the same, first posterior cell open. Pubescence and pollen as in that species. The proboscis is rather shorter, from palpi to tip about once and a fourth the eye-height. The ventral plate is very different from *Z. intermedium*, and similar to that of *Z. fulvifrons* (*abitus*) being low, much broader than high, and behind with a very broad, dark striated area.

Length, 6 mm.

From Falls Church, July and Sept., and Mt. Jefferson and Horse Lake, Oregon, July (Lovett). Males from Mt. Graybeard, N. Car., May, and La Quintina, Cal., probably belong here. I have named it in honor of him whose description of *Z. fulvifrons* was sufficiently accurate to enable me to describe this form.

Zodion occidentale n. sp.

Face whitish; front golden, darker on the vertex, with the dark spots on the middle toward the antennæ; occiput largely black; antennæ reddish, third joint as long as the second, arista black; thorax brownish gray, with the usual stripes distinct, except the median one, which is faint. Abdomen brownish gray, paler near tip, indistinct blackish spots near middle; legs yellowish, femora often blackish above; tarsi darker, last joint black. Wings gray hyaline, veins dark. Vertex thorax, abdomen and legs clothed with rather long, black hair. Cheeks more than one-half eye-height; proboscis rather short. Ventral plate a little longer than broad.

Length 7.5 to 9 mm.

From Montaville, Mary's River, and Corvallis, Oregon, May and July (Lovett). Cotypes in collections of Oregon Agricultural College and that of author.

Zodion obscurum n. sp.

Face whitish, front golden, a brown median stripe reaching forward from the ocelli; antennæ reddish, arista mostly pale, third joint fully as long as the second; occiput mostly black. Thorax black,

gray pollinose, not showing distinct stripes. Abdomen black, gray pruinose, last segment red, hypopygium reddish on basal part, black on apical part; legs yellowish, tarsi darker. Wings nearly hyaline, venation mostly black. Vertex, thorax, abdomen and legs clothed with black hair. Cheeks hardly one-third of eye-height; proboscis moderately long; first posterior cell open. Ventral plate very broad.

Length, 5.7 mm.

From Bear Valley, San Bernardino Co., 6700 feet, and Santa Monica, both Cal. (Clark). Type in collection of author.

Zodion reclusum n. sp.

Face pale yellowish white; front golden, vertex brown, limited transversely in front, antennæ reddish, arista black, third joint about as long as the second; thorax brownish gray, with the fine stripes brown, the submedian very short, the lateral indistinct. Abdomen yellowish gray, with brown marks near middle, leaving a pale median stripe, basal segment gray; legs yellowish, femora usually blackish above. Wings brownish, venation mostly black. Vertex, thorax, abdomen and legs clothed with black hair. Cheeks not one-third the eye-height.

Length 6.5 mm.

From Redlands, Cal., Nov. (Cole) and Corvallis, Oregon, (Bridwell). Cotypes in collections of Oregon Agricultural College and that of the author; both males.

Zodion lativentre Graenicher.

I do not know this species. A male of what I have called *Z. perlongum* was sent Dr. Graenicher for comparison, but he said his species was very different from it.

Zodion abdominale Say.

The size is given as smaller than *Z. fulvifrons (abitus)*, and the abdomen pale like the femora. This agrees well with *Z. bicolor* Adams; moreover, Say's statement about the color of the veins fits this species particularly well. The thoracic marks also agree.

Zodion triste Bigot.

Bigot says little of marks on thorax, and I have identified as this species provisionally a form from the West, which is small, has dark legs, and almost unmarked thorax.

Myopa.

In the following table of the species in my collection I have depended largely upon color; the color of the hair is very important; but the amount of reddish on thorax and abdomen in certain species is doubtless variable.

1. Wings with distinct dark clouds over the cross-veins; abdomen black-haired .2
   Wings without clouded cross-veins.......................................4
2. Face with rather short hair; a cloud in first posterior cell, which is closed,
   small species...*melanderi*
   Face with long white hairs, forming a fringe below; first posterior cell open. .3
3. Face with several small black spots on each side, dark clouds in both first
   and second posterior cells...*willistoni*
   Face at most with a reddish spot each side above, no clouds in posterior cells.
   vicaria
4. Thorax and abdomen with short appressed white hairs...................5
   Thorax and abdomen with black hair..................................6
5. Abdomen mostly reddish; costal cell not much darkened, *vesiculosa var.varians*
   Abdomen mostly black; costal cell very plainly blackish..........*vesiculosa*
6. The hairs on thorax above are hardly one-half as long as the arista; abdomen
   also with very short hair..7
   The hairs on thorax above as long as the arista; abdomen also with long
   hair...9
7. Abdomen wholly red; hairs of body are extremely short..........*seminuda*
   Abdomen largely black...8
8. Abdomen reddish on sides and behind; fifth segment not divided by a median
   pollinose pale streak...*plebeia*
   Abdomen not reddish; fifth segment with a median stripe of pale pollen.
   virginica
9. Abdomen mostly black...*longipilis*
   Abdomen mostly red...10
10. Proboscis very long, the second joint as long as femur I, the last joint as
    long as the second..*clausa*
    Proboscis with the second joint only about two-thirds as long as the front
    femur, the last joint a little shorter than second................*rubida*

Myopa vesiculosa Say.

This species is readily known by the white hair of body; it occurs both East and West, specimens are before me from Washington State, and the *conjuncta* of Thompson from California may possibly be the same species.

Myopa vesiculosa var. **varians** n. var.

Structurally like the typical form, but rufous throughout, and the wings lack the dark cloud through the middle area. The antennæ are a trifle shorter, but this may not be constant.

From Lincoln, Neb. Sent me by Mr. P. R. Jones as his idea of *Myopa clausa*.

Myopa vicaria Walk.

The description of *M. pilosa* Will. fits this species very well, but I have not seen any Californian examples and it may be distinct.

Myopa willistoni n. n.

M. pictipennis Will. preoccupied by *M. pictipennis* Rob.-Desv. 1830.

This species is distinct from all our other forms, except *melanderi*, by the much thickened femora. The second joint of proboscis is fully two-thirds of the head-height, the third joint is about equal to the second. The hair on the face is not as long as in *vicaria*. The knob of the halters is dark, pale in our other species. I have seen specimens from Oregon and California.

Myopa melanderi n. sp.

Black, face white, with short white hair, front with the usual black V-mark, and spots at the base of the antennæ, latter dark. Head from in front about circular; cheeks scarcely higher than eyes; proboscis black, last joint shorter than second, the latter hardly two-thirds of head-height; second antennal joint scarcely if at all longer than the third. Thorax black, two short, white pollinose stripes in front part. Abdomen, black, posterior margin of segments narrowly white pollinose, rather broader on the sides, a narrow, median, white pollinose stripe over all segments, last segments with only a pair of small dark spots. Legs black, base and extreme tip of femora, base, middle and tip of tibia and the tarsi pale. Front, thorax, abdomen and legs with moderately long black hair. Wings gray, yellowish on base and near stigma; anterior and posterior cross-veins plainly broadened with blackish, and a distinct rounded cloud above the posterior cross-vein in the first posterior cell, latter closed before tip. All femora much thickened as in *M. willistoni.*

Length, 4.5 mm.

From Pullman, Wash., 6 May (Melander).

Myopa clausa Loew.

I have considered as this species a reddish form with extremely long proboscis; it occurs in the East, and I have two from Utah (Spalding), also one from Mt. Graybeard, N. Car.

Myopa longipilis n. sp.

Black, face yellowish white, with fairly long white hair; front brown, showing the usual V-mark; antennæ dark, second joint a little longer than the third; head from in front almost circular; in some specimens a faint dark cloud on each cheek; proboscis black, second joint about two-thirds of head height; third joint about equal to the second. Thorax rather reddish on sides and behind; abdomen reddish toward tip, or on the sides, some of the segments narrowly white pollinose on sides behind. Legs reddish, on the femora largely blackish, except base and tip, tarsi pale. Front, thorax, abdomen and legs with long black hairs, fully as long as in *M. vicaria.* Wings rather pale brownish yellow, without dark clouds.

Length, 9.5 mm.

From Pullman, Wash., April and May (Melander).

Myopa seminuda n. sp.

Face yellowish white, with short white hair, antennæ and front reddish, second joint of antennæ much longer than the third which is usually short; front with the usual brown marks; occiput with large black mark behind each eye, head from in front plainly higher than broad, cheeks fully eye-height; proboscis with second joint not two-thirds of head height, third about equal to second. Thorax red, with three broad black stripes, more or less broken, middle one with a median pale line; metanotum deep black; abdomen bright red, lateral margins of segments barely white pollinose behind. Legs red, tarsi yellowish. Front, thorax and abdomen with extremely short, erect black hairs. Wings brownish, base yellow, costal area also rather yellowish, first posterior cell open or closed.

Length, 9 mm.

From Corvallis, Ore., June, and near base of Mary's Peak, Ore., May (Lovett), Cotypes in Coll. author and Ore. Agric. Coll. The extremely short hair distinguishes the species.

Myopa virginica n. sp.

Black, head yellowish white, face with short white hair; antennæ reddish, second joint much longer than the third; front with dark V-mark extending back and down on the occiput, also in a V. Head from in front plainly higher than broad, cheeks equal eye-height; proboscis dark, last joint paler, and as long as the second, latter about one-half of head height. Thorax with humeri shining, sometimes faintly reddish on sides and behind; abdomen black, first and second segments with lateral white pollinose spots, third fourth and fifth with apical white pollinose margin, broader at the sides, sixth and seventh mostly white pollinose; fourth and fifth segments with a narrow median white pollinose stripe. Legs blackish or brownish, basal part of tibia and most of tarsi pale. Front, thorax, abdomen and legs with rather short, black hair. Wings brownish, base yellow, first posterior cell closed before the margin.

Length, 7 mm.

From Falls Church and Glencarlyn, Va., in June and early July. Also one from the Catskill Mountains, N. Y., June, and one from Black Mountain, Swannanoa Valley, N. C., May. Probably this is the form referred to by Williston in his remarks after the description of *P. vesiculosa* as one specimen from Virginia with black pile.

Myopa plebeia Will.

Described from Arizona, I have seen one from Washington State (Mann.) Although structurally similar to *M. virginica*, it is much larger, and with a very different habitus, however too few specimens are known to me to know if it varies. The *M. castanea* of Bigot is quite probably the same form.

BIGOT'S SPECIES.

G. rubida.

Agrees with a form of *Myopa* common in the West which is close to *M. clausa*, but with a shorter proboscis. I have it from Oregon and Washington.

G. maculifrons.

This is probably *Myopa vesiculosa* which also occurs in the West. The only objection is that Bigot says the hair of thorax is brown (he does not say black).

G. castanea.

Is larger than his other species; the red abdomen, black above, would indicate that it is *plebeia* Will., which agrees also in other characters. Von Roeder's statement that it is *Myopa clausa* is based on the idea that the closed cell is a specific character.

Occemyia abbreviata Lw.

The abdomen of both male and female slightly clavate, whitish on the posterior sides of second segment; hair black; in the female the ventral plate is very broad, low, and dark colored. Hind femora are often pale on basal half, black on apical half. The pollinose marks of abdomen are whitish. The size varies, and three specimens are as small as the smallest *O. loraria*.

Occemyia loraria Lw.

In the male the abdomen is more elongate and cylindric than in *O. abbreviata;* the pollinose marks more yellowish, the hair also yellowish. In the female the ventral plate is narrow, and mostly pale colored. The size varies, and some specimens are as large as the largest *O. abbreviata*. From Oregon (Corvallis) I have seen specimens that I cannot distinguish from the Eastern ones.

Dalmannia pacifica n. sp.

Face pale; in the male a large elongate dark spot each side just outside of the facial ridges, in female wholly yellowish; vertex and front black; thorax shining black, the humeri and scutellum yellow. Abdomen mostly yellowish above and below; first segment black, with a pale band at base and apex broadly pale; segments two and three yellow, with four separated (or barely connected) black spots across base, the lateral spots reaching the side margins; fourth segment yellow, with a black spot on each side, in the female the fifth segment has a pair of black stripes, united behind, and the ovipositor black; venter with a middle black spot on first segment; legs yellow, tarsi black; front and

hind femora with some black, mostly above; wings brownish; halters yellow. In structure very close to *D. nigriceps* and *D. picta;* in the venation the second vein ends nearer to the first vein than in *D. picta;* in this respect similar to *D. nigriceps.*

Length, 7 mm.

From Corvallis, Oregon, 4, 6 June (Lovett). Cotypes in collection Ore. Agr. College and that of author. Differs at once from *D. picta* and *D. nigriceps* in the much greater extent of the yellow on the abdomen.

Our four species may be distinguished as follows:

1. Humeri dark;scutellum dark; small species.......................*vitiosa*
   Humeri pale, scutellum more or less pale.................................2
2. Second and third segments yellow with four basal black spots; scutellum
   yellow..*pacifica*
   Second and third segments mostly black, with apical yellow margin, more or
   less indenting the black...3
3. Scutellum yellow; Eastern species..............................*nigriceps*
   Scutellum mostly dark; Western species.........................*picta*

LOCAL SPECIES.

The following eighteen species have been taken in Northern Virginia at, or in the vicinity of, Falls Church. Of the eighteen, thirteen have been taken in June, two (*Myopa*) only before June, and three only later than June. Almost invariably they occur only on white blossoms; *Myopa* in early spring has been taken on red bud, but prefers amelanchier.

Physocephala tibialis Say. Fairly common, 14 June to 17 Sept.
Physocephala sagittata Say. Falls Church, 17 June to 8 July.
Conops brachyrhynchus Lw. Falls Church, 16 June to 6 July.
Conops xanthostomus Will. Falls Church, 5 July to 8 Sept.
Conops sylvosus Will. Falls Church, 9 May to 15 July.
Myopa vicaria Walk. Falls Church and Great Falls, 15 April to 27 May.
Myopa vesiculosa Say. Falls Church and Great Falls, 10 to 27 April.
Myopa virginica Bks. Falls Church, 15 June to 7 July.
Occemyia abbreviata Loew. Common, 22 May to 31 July.
Occemyia loraria Loew. Common, 14 June to 18 Sept.
Zodion fulvifrons Say. Common, 13 June to 24 Sept.
Zodion perlongum Coq. Falls Church, 6 to 21 Sept.
Zodion sayi Bks. Falls Church, 6 July to 27 Sept.
Zodion nanellum Loew. Two from Falls Church, Great Falls, 16 June, 7 Sept.
Zodion parvum Adams. Three from Glencarlyn, 24 June, 2 July.
Dalmannia nigriceps Loew. Great Falls, Glencarlyn, 5 and 7 June.
Dalmannia vitiosa Coq. Falls Church, Glencarlyn, 14 and 17 June.
Stylogaster neglectus Loew. Falls Church, Great Falls, Glencarlyn, 14 June to 27 July.

THE REFLEX "BLEEDING" OF THE COCCINELLID BEETLE, EPILACHNA BOREALIS.

N. E. McINDOO, Ph. D.,
Bureau of Entomology, Washington, D. C.

INTRODUCTION.

It is a well-known fact among entomologists that when disturbed certain coccinellid and meloid beetles fold the antennæ and legs against the body, eject small drops of liquid from the femoro-tibial articulations and feign death. There has been quite a controversy as to how the liquid is expelled so quickly and as to whether the liquid is blood or is a glandular secretion. Those who believe that the liquid is blood fail to show how it passes through the articular membrane to the exterior, and those who think that the liquid is a glandular secretion do not conclusively prove their view and they fail to explain how such a large quantity of the secretion can be expelled so quickly.

The phenomenon of ejecting liquid from the femoro-tibial articulations has been called "reflex bleeding." The object of the present paper is to show that the phenomenon is a true reflex, but that instead of the liquid being blood, it is a secretion from hypodermal glands and that it passes to the exterior through innumerable tubes opening near and in the articular membrane.

To obtain material for sections, adult beetles that had been kept in the laboratory all summer were mostly used, although two beetles emerged a short time were also used. Most of the sections were cut five microns in thickness, and all of them were stained with Ehrlich's hematoxylin and eosin. In regard to more details concerning the technique, the reader is referred to the writer's work (1915) on "The Olfactory Sense of Coleoptera."

EXAMINATION OF LIVE BEETLES.

When live individuals of *Epilachna borealis* are examined without irritation under a low-power lens, they appear wet. The more the beetles are irritated the wetter their integuments become. The entire chitinous integument is more or less covered with small yellow flakes. On the legs and elytra these flakes are numerous, and they may be easily removed with a needle. Beetles in the field eject small drops of liquid from the

femoro-tibial articulations when only slightly irritated, but after they have been handled and kept in captivity for a short time a stronger mechanical stimulus is necessary to cause them to force liquid from the articulations. Beetles kept in confinement four months with plenty of pumkpin leaves and water were tested to ascertain how many drops of liquid a leg is able to expel in rapid succession. A hind leg was able to eject as many as six small drops with only a few seconds intervening between the emission of any two of them. A middle or front leg was not able to eject quite so many drops. Under a low-power lens the liquid seemed to come from the articular membrane and from the extreme proximal end of the tibia. Each time the leg was irritated a much smaller drop was also seen on the first tarsal joint.

To determine the strength of the mechanical stimulus required and the mechanics employed in ejecting the liquid to the exterior, beetles were placed on their backs under a low-power lens. When the distal end of a femur was gently touched with a needle, a muscular contraction instantly folded the tibia against the femur, and a small drop of liquid appeared simultaneously at the articulation. The drop always increased slightly in size after first appearing. A stronger stimulus with the needle was required to bring about the emission of each succeeding drop. The sixth drop, the smallest of all, was produced only by rubbing the entire femur hard with the needle. Legs with the tibiæ folded against the femur can also eject the liquid, but not so easily. Muscular contractions may be noticed in them. Legs held out straight are also able to eject the liquid, but with much difficulty, and muscular contractions are very evident.

The liquid ejected has an amber color and a very offensive odor. It is almost as bitter as quinine and when tasted, a bitter taste lingers in the mouth for almost a half day. It is slightly viscid and dissolves slowly in water. In order to compare it with blood entirely free of any hypodermal glandular secretion, the wings of the same live beetles were cut in two. It will later be shown that the wings do not contain any hypodermal glands, but they are full of blood. Blood from the wings has the same color, the same taste and probably the same odor as the ejected liquid, but the blood is not viscid and it dissolves readily in water and does not sink as quickly as the ejected fluid.

DISTRIBUTION OF HYPODERMAL GLAND PORES.

In order to study the distribution of the pores through which the liquid presumably comes, causing the integument to be wet, several specimens were treated with caustic potash twenty-four hours. When removed from the caustic potash, all the tissues were disintegrated leaving only the chitinous parts. When thoroughly washed with water the chitinous integuments were carefully examined.

Minute pores were observed in the chitin of the thorax, abdomen, legs and elytra. The wings contain none of these pores and the head with its appendages were not examined. A single pore (Figs. 1, 6 and 7, p) usually lies near the base of each hair, but sometimes two pores may be seen near the base of a hair. Sometimes a pore lies against the hair socket (Fig. 7, sk). When the pores are more numerous than the hairs, they are grouped together and are not associated with the hairs. The pores are most abundant on the legs (Figs. 1 3, p). Besides most of the hairs on the legs being associated with pores, four groups of this type of pore lie near the femoro-tibial articulation and these pores are also grouped together on the tarsal joints. For this reason the region around the femoro-tibial articulation (Fig. 1) contains the most pores of any part of the integument. The first tarsal joint (Fig. 2) contains less and the fourth tarsal joint (Fig. 3) is least well supplied with pores. The thorax (Fig. 6) and the dorsal side of the elytron (Fig. 7) are well supplied with pores, but here the pores are associated with the hairs and are never grouped together.

Another type of pore was found. While examining the articular membranes (Fig. 1, $artm$) of the femoro-tibial artic-ulations, many minute pores were seen in them. This is the first time that pores are reported in the articular membrane.

The group of pores (Fig. 1, a) always present on either side of the proximal end of the·tibia is oval in shape and the chitin containing the pores is lighter in color than the surrounding chitin. In counting the pores in the groups, all the legs of five individuals were used. The number of pores in the groups on the tibæ of the front legs varies from 14 to 25 with 17 as an average; on the tibiæ of the middle legs from 13 to 30 with 20 as an average; on the tibiæ of the hind legs from 18 to 28 with 23 as an average. The general average number of pores in these groups for all three pairs of legs is 20.

The group of pores (Fig. 1, *b*) at the distal end of the femur and near the articular membrane is arranged in a manner more or less like a string of beads (Fig. 4).   A group is present on either side of the articular membrane, but both groups on the same femur can never be seen because one of them always lies under a portion of the femur.   For this reason the pores in only about a half of these groups were counted.   On the front legs the pores vary from 24 to 26 with 25 as an average; on the middle legs from 24 to 37 with 30 as an average; on the hind legs from 29 to 38 with 32 as an average.   The general average number of pores in the groups on the femurs of all three pairs of legs is 30.

On account of the opaqueness of the articular membrane and the small size of the pores found in this membrane, these pores can not be counted, but they are estimated as from 200 to 500 for each membrane

Since the four groups of pores near the articular membrane and those in the membrane are the only openings, besides a few olfactory pores (Fig. 1, *olp*) and the pores associated with the hairs, which pass through the chitin at the femoro-tibial articulation where the drop of liquid appears, we must conclude that these pores are the only passages through which the liquid is ejected to the exterior.   Counting only the pores in these groups and those in the articular membrane, we see that each tibia has 40 pores, each femur 60 pores, and each articular membrane perhaps 400 pores, making about 500 pores through which the liquid issues.   Since all of these pores are so close together the liquid from all of them unites into a drop, while a drop is never seen elsewhere except on the first tarsal joint where there are also many pores near one another.

<center>STRUCTURE.</center>

In the preceding pages it is shown that the liquid ejected passes through pores in and near the articular membrane.   In the following pages it shall be determined whether the liquid ejected is blood or a glandular secretion.

1.   External structure.

When observed under a high-power lens, the pores in the groups and those associated with the hairs appear as very small light spots.   In a vertical view each light spot (Fig. 3, *p*) is

bordered by a dark circle inside of which appears a transparent spot that is bordered by a much smaller circle. The internal anatomy of a pore (p. 206) shows what these various parts are. In oblique views the inner circles (Figs. 2, 4 and 5) appear as small wedge-shaped figures.

The pores vary considerably in size. All of those on the tibia (Figs. 1 and 5), all of those associated with hairs on the femur (Fig. 1), and those on the thorax (Fig. 6) and elytron (Fig. 7) are of about the same size. Those in the groups on the femur (Fig. 4) are comparatively large, while those on the tarsus (Figs. 2 and 3) are medium in size. Any one of these pores is several times smaller than an olfactory pore (Fig. 1, *olp*). The pores in the articular membrane (Fig. 8, *pl*) are about equal in size to the inner circles of the other type of pore. The tubes connecting with these pores have the same size.

2. *Internal structure.*

Sections through all the foregoing enumerated pores, except those in the articular membrane, show that this type of pore is connected with reservoirs. And furthermore, since both types of pores are the external openings of hypodermal glands, these structures may be designated hypodermal glands with and without reservoirs.

(a) *Hypodermal glands with reservoirs.*

There is a great difference in appearance between the hypodermal glands in old adult beetles and those in beetles emerged a short time.

(1) *Mature hypodermal glands.*

In sections through this type of gland, that part of the structure to be noticed first is the reservoir (Fig. 9, *r*). It appears as a round or slightly oblong, light-colored cavity. An efferent tube (*e*) runs from the surface of the chitin into the reservoir and ends about one-third the distance from the bottom of the reservoir. A dark-staining, granular substance is usually seen around the end of this tube in the reservoir. It is now easily seen that the diameter of the light spot in a superficial view is equal to the diameter of the reservoir, and that the transparent spot surrounded by a much smaller circle is the same as the outer opening of the efferent tube. This opening is in reality the pore.

Just beneath the reservoir lies the pore canal (*pc*) which is usually narrower than the diameter of the reservoir.

Lying in the hypodermis just beneath the pore canal lies . the large gland cell (*glc*). On account of its size and the way the hypodermal wall (Figs. 20 and 21) bulges around it, this cell is much more conspicuous than the hypodermal cells. In fact the walls of the hypodermal cells can not be recognized but their nuclei (Fig. 20, *hnuc*) are distinct. The nuclei of the gland cells (Fig. 9, *nuc*) are larger than those of hypodermal cells. They are usually round while those of the hypodermal cells are oblong. They generally lie in the broader ends of the cells. Their nucleoli (*nucl*) are always distinct. The cytoplasm (*cyt*) is more or less granular. Lying either near the center or in the narrower end of the cell there is a transparent, round area, the ampulla (*am*), which is usually larger than the nucleus. The ampulla appears to contain radial lines, but on account of the small size of the cells, these lines are almost indiscernible. At the center of each ampulla is always distinctly seen the free end of the conducting tube (*c*) whose walls at the free end are darker than elsewhere. Sometimes a dark circle is seen at the center of the ampulla, showing that the conducting tube has been cut in two. This fact shows that the tube is really hollow and is not solid. The conducting tube leads from the center of the ampulla through the pore canal to the reservoir where its walls unite with the walls of the mouth of the reservoir.

The gland cells vary considerably in size. The largest ones (Fig. 18, *glc*) are associated with the groups of pores at the distal end of the femur. Those in the elytra are about as large as those widely distributed in the legs.

The reservoirs and pore canals (Figs. 10 and 11) also vary considerably. The reservoirs in the femur near the articular membrane (Fig. 19) are the largest. The pore canals and conducting tubes depend in length on the thickness of the chitin (Figs. 10 and 11) which varies much.

In order to ascertain if the efferent and conducting tubes are chitinous, fresh material containing the femoro-tibial articulations was treated in caustic potash four hours. A study of the sections made from the material thus treated showed that these tubes are composed of chitin (Fig. 12, *e* and *c*).

(2) Origin of hypodermal glands with reservoirs.

In regard to the formation of the reservoirs and efferent tubes nothing can be said, because they are fully developed when the insect emerges, and no younger stages were preserved in fixing fluids.

When the insect has been emerged an hour, the chitin is about one-third developed. This is seen by comparing Figures 11 and 13. Figure 11 is from an old adult, and Figure 13 is from a beetle emerged one hour. The darker-colored chitin (Figs. 10 and 11, ch_1) is formed before the insect emerges and the lighter-colored chitin (ch_2) is formed after the beetle emerges.

When the insect has been emerged an hour, the gland cells vary in development from undifferentiated hypodermal cells to almost fully developed gland cells. At this stage the hypodermis (Fig. 13, h) is comparatively thick and the hypodermal cells (hc) appear as dark-staining nuclei without the cell walls being visible. The first stage in the formation of a gland cell may be represented by a large hypodermal cell at the mouth of a reservoir (Fig. 13, hc). The second stage is represented by a hypodermal cell that has enlarged sufficiently to cause the hypodermal wall to bulge outward. Its nucleus is now comparatively light in color, its cell wall is discernible, and its cytoplasm is darker than that of the hypodermis. Figure 14, glc, represents such a stage.

The third stage in the development is represented by a gland cell that is forming the conducting tube. All the steps during the formation of the conducting tube were not seen, but enough were observed to imagine the full procedure in the development. A gland cell in the second stage of development is round, or slightly oblong. Now it begins to elongate rapidly and one end begins sending out a process. At this step the ampulla appears and the free end of the conducting tube is formed. The conducting tube is formed from the cellular secretion as rapidly as the process of the cell grows in length. Since the tube at this step often appears as a single dark heavy line instead of two parallel lines, it is probably laid down as a rod of secreted substance rather than as a tube, but later it becomes cylindrical. Gland cells with processes (pr) of various lengths are shown in Figures 15 to 17. One process (pr) shown in Figure 17 has actually entered the mouth of a reservoir. Now it may be

imagined that the protoplasm at the tip of the process with-
draws and the peripheral end of the tube unites with the walls
of the mouth of the reservoir.

By the end of the third stage of development, the gland cells
are probably fully developed in size (compare Fig. 16, *glc*, and
Figs. 9 and 10, *glc*), but they certainly do not function as gland
cells until all the chitin is developed.   The thicker the chitin
becomes, the longer the pore canals and conducting tubes
must be, and the farther the gland cells must migrate into the
lumen of the appendage.   Up to the time of the fully developed
chitin, the gland cells, instead of producing a glandular secre-
tion, produce a chitinous secretion to form the conducting tubes.
Perhaps the withdrawal of the protoplasm from the tip of the
cell process keeps pace with the lengthening of the pore canal, so
that by the time the chitin is fully formed there is no protoplasm
surrounding the conducting tube.   Now, instead of the gland
cells standing more or less vertically to the chitin, they lie
parallel to the chitin, and the conducting tubes no longer enter
the tips of the narrower ends of the cells, but they enter the
sides of the cells usually about midway between the two ends.

(b)   Hypodermal glands without reservoirs.

In a section through the articular membrane (Fig. 18, *artm*),
may be seen one or more small tubes.   These are the conducting
tubes (c_1) observed in chitinous preparations as shown in
Figure 8.   They are so small and so transparent that they
were not noticed until after this piece of work was almost
completed.   For this reason, it is not surprising to know that
other investigators have overlooked them.   They have no res-
ervoirs.   Each one pierces the chitin and terminates (p_1) on the
surface of the flexible and comparatively thin articular
membrane.

A layer of peculiar hypodermal cells had been noticed beneath
the articular membrane for some time before the conducting
tubes had been observed, but these cells were not given any
particular attention until the conducting tubes had been dis-
covered.   A careful study of these cells (Fig. 18, glc_1) under the
highest lenses soon showed that they are gland cells like the
ones already described except they are several times smaller.
Since they are so small their internal structures can not be
studied critically.   A conspicuous nucleus is always present, but

the ampulla is generally indiscernible and no tubes were seen
running into the cells, although it is common to see the free
ends of the tubes among the cells.   That no tubes were seen
entering the cells is easily explained by supposing that they
were pulled out of the cells by the hypodermis withdrawing
from the chitin during the fixation.   The injury produced by
the tubes being pulled out of the cells is certainly the cause of
the ampullæ being rarely seen.   While examining live gland
cells in the honey bee, the writer (1914) found that the slightest
injury to the cells caused the ampullæ to disappear.

At certain places the gland cells (Fig. 21, glc_1) lie bead-like
in the hypodermis, causing the hypodermal wall to bulge out
around each of them, while at other places they lie in groups
(Figs. 18, 19 and 21 glc_1) among the cells belonging to the other
type of hypodermal glands.

(1)   Origin of hypodermal glands without reservoirs.

Since no material of pupæ was prepared, little can be said
about the origin of these glands, because the conducting tubes
are fully developed and the gland cells are being rapidly formed
when the insect emerges.   When the insect has been emerged an
hour, large hypodermal nuclei (Fig. 19, *hnuc*) may be seen
beneath the articular membrane, and many small cells, pre-
sumably gland cells (glc_1), lie in and below the hypodermis
among larger gland cells (glc).

There is no doubt that these gland cells are modified hypo-
dermal cells, but since the conducting tubes pierce the entire
thickness of the chitin, they must have been formed simul-
taneously with the chitin.   The conducting tubes belonging to
hypodermal glands of the same type in the honey bee are
formed as follows: Just before the hypodermal cells begin
secreting the chitin, some of them begin sending out processes
into the lumen of the abdomen.   At the same time other hypo-
dermal cells migrate into the lumen and the processes sent into
the lumen unite with the cells that have migrated inward.
Each process forms a chitinous tube which runs from the ampulla
to the surface of the chitin.   By the time the chitin is fully
developed, the gland cells are also fully developed, the proto-
plasm in the processes has been withdrawn from around the
tubes, and the tubes are firmly embedded in the chitin.

HOW REFLEX "BLEEDING" IS ACCOMPLISHED.

The lumen in the extreme proximal end of the tibia is divided into two almost equal chambers (Fig. 20, *bs*) by a membrane (*h₁*) extending across the leg. In structure and general appearance this membrane resembles the hypodermis with which it unites on each side of the leg. In that chamber containing the nerve (*n*) and trachea (*tr*) lie only a few scattered gland cells and only a small amount of blood may be seen in it. The other chamber is full of blood and it is the one that contains all the gland cells (*glc*) belonging to the two groups of pores found on the tibia. No muscles are seen in the tibia at this place.

The lumen in the extreme distal end of the femur is likewise divided into two chambers by a membrane. In sections passing through the articulation, may be seen muscle fibers (Fig. 21, *m*) at the extreme distal end of the femur, tracheal branches (*tr*) running to the gland cells (*glc*), and a nerve (*n*) running through the center of the articulation. All the space not filled by the preceding structures may be called blood sinuses (*bs*).

Under ordinary conditions in the natural environments of the beetles all the reservoirs, conducting tubes and ampullæ are possibly kept constantly full of the glandular secretion. It is reasonable to think that all parts of the cytoplasm of the gland cells are slowly and constantly producing a secretion that flows into the ampullæ from which it gradually passes through the conducting tubes to the reservoirs, if present, from whence it passes through the efferent tubes to the exterior. On the surface of the chitin the secretion forms a small circular film around the exit of each pore. Since this secretion is quite volatile and has an offensive odor, perhaps no further discharge of the secretion is necessary to guard off most of the enemies of this insect. During the constant discharge of this secretion no reflex is called into play.

Since a pore lies near the base of each hair, and as many of these hairs are innervated, a correlation between each tactile hair and the pore near it might at once be suspected. To imagine that the pore lies near the hair for mere protection is not sufficient correlation, because the innervation of the hair would not be needed, if only the protection of the pore is considered. A little speculation, therefore, may not be out of

place. When a tactile hair is touched, its sense cell is stim-
ulated. Since the sense cells lie near and sometimes against the
gland cells, the former may in some unknown way stimulate
the latter. If such should be the case, then the gland cells
would begin vigorously at once to produce more secretion.
And as a result much more liquid would be discharged than
ordinarily. If such a relation exists between the gland cells
and tactile hairs, the writer can think of no simple reflex better
adapted for protecting the insect.

Considering the discharge of liquid at the femoro-tibial
articulation, there is no question about the reflex, but whether
the stimulus is brought about by pressure on the chitin or by a
stimulation of several sense cells belonging to tactile hairs, is an
open question. Since only a slight mechanical irritation at the
distal end of the femur is required to cause a discharge of the
secretion, it is more reasonable to think that the stimulation
is brought about by the tactile hairs than by the pressure on
the chitin. As soon as the tactile hairs are touched, the muscles
contract folding the tibia against the femur and forcing the
blood into the chamber containing the gland cells. At once
the gland cells are put under a high blood pressure which
immediately stimulates them. Instantaneously they discharge
all the secretion in their ampullæ causing the secretion in the
reservoirs to be shot to the exterior. Now the gland cells
without reservoirs play their part by immediately increasing
the size of the drop of discharged liquid. Causing drops to be
discharged may be continued until the gland cells become
exhausted which really occurs after the fifth or sixth drop has
been expelled. Each drop is smaller and is discharged less
quickly than the preceding one. This shows that the supply
of liquid is limited from the beginning, and that a little more
time is required for producing each succeeding drop than the
preceding one, but if the liquid were blood such would not be
the case. It would seem that the liquid secreted under such an
emergency would not be exactly the same in composition as
that which is produced when the cells are not overworked, but
under normal conditions it is perhaps never necessary for these
insects to exhaust this glandular secretion.

From the preceding it is evident that the phenomenon of
ejecting liquid from the femoro-tibial articulation is a true
reflex, but instead of the liquid being blood, it is a hypodermal

glandular secretion, instantaneously discharged to the exterior under a high blood pressure which is caused by a muscular contraction, forcing the blood into a specially devised chamber containing the gland cells. It is, therefore, seen that the membrane extending across the lumen of the leg plays an all-important part in the discharge of the secretion, because if it were not present the blood would occupy too much space and could not be put under a sufficiently high pressure to stimulate all the gland cells simultaneously. Furthermore, since the nerve and trachea lie in the chamber containing only a few scattered gland cells, this may also be a device for protecting these structures against a high blood pressure.

FUNCTION OF THE HYPODERMAL GLANDULAR SECRETION.

On account of the bitter taste, the high volatility and the offensive odor of this secretion, there is no doubt that its primary function is that of protection. Since we know very little about the ability of the lower animals to distinguish colors, we can not attribute any protecting significance to the color of this secretion, chiefly because the bright amber color is noticed by a person only when drops are ejected from the femoro-tibial articulations. Since these drops are so inconspicuous, it is doubtful whether they are ever seen by an enemy even as large as a bird. Nevertheless, it is quite probable that the amber color is associated with the taste and odor of the secretion.

If the bitter taste of the secretion serves as a means for protecting the insect, it must be granted that the animal seizing the insect can taste and that the secretion in stimulating the gustatory organs of the enemy causes an "unpleasant" sensation. We are certainly safe in saying that the vertebrate enemies (particularly birds) of this insect experience an offensive gustatory sensation when they attempt to eat these beetles. To say that such a sensation is experienced by its insect enemies can not be emphasized, because it has never been conclusively proved that insects can taste.

Since we know that insects as a rule have an acute sense of smell and that the higher animals are also endowed with an olfactory sense, we are safe in assuming that the offensive odor of the secretion is sufficient in most cases to guard off the enemies of this insect. This statement is supported by the fact that most of the common, strong odors, whether pleasant or unpleasant to us, act as repellents to insects.

The taste, volatility and odor of the secretion seem to be due to a peculiar principle called cantharidine, which is a volatile, acrid, bitter solid, crystallizing into four-sided prisms. It is thus seen why the liquid evaporates so quickly when ejected, leaving yellow flakes on the integument.

A few investigators have performed many experiments with various warm and cold-blooded animals by feeding them some of the secretion. De Bono (1889) used many insects, frogs, toads, guinea pigs and coyotes. He found that the secretion from *Timarcha pimeliodes* has a manifest action on the heart of warm and cold-blooded animals, and that it has an injurious effect on *Musca communis, Sarcophago carnaria*, although little or no injurious effect on other insects. Lutz (1895) remarks that the secretion from the same insect may kill flies within a few minutes and is poisonous for warm and cold-blooded animals. Porta (1903) fed the secretion from *Coccinella 7-punctata* to various animals. He says that the liquid exercises a poisonous influence upon the organism of both warm and cold-blooded animals, and his experiments show that it is injurious to the brain. He found, however, that it does not exercise any influence upon insects. For *Coccinella* he thinks that the secretion probably serves as a means of defense by the odor which is offensive to other insects and perhaps this yellowish liquid indicates to them a harmful substance.

The odor of the secreted liquid, besides serving as a means of defense, probably also serves as a means for individual and sexual recognition. The secretion of a given species perhaps emits a specific odor by means of which the different individuals and sexes of that species recognize one another.

DISCUSSION.

Lacordaire (1838) was one of the first investigators to describe the phenomenon of ejecting liquid from various parts of the body of certain insects. He says that when *Dytiscus* and *Gyrinus* are picked up, they emit through the articulations between the head, thorax and abdomen a milky and fetid fluid. *Meloe* emits from the articulations of the legs a yellowish-orange liquid whose odor is not disagreeable. Coccinellidæ and Chrysomelidæ emit an analogous liquid at the same places, but it has a different odor and is quite strong.

The ejection of a liquid from the articulations of the rudimentary wings of certain Orthoptera has been studied by Cuenot (1896a) and others.

Izquierdo (1896) says that liquids discharged by insects as a means of defense may be divided into three groups: (1) Those from organs which are furnished with glands. Such organs are found in all the families of insects and their exits may be found in the thorax, abdomen, at the anus or in the last portion of the intestine; (2) liquids which are discharged from the femoro-tibial articulations; and (3) liquids that are discharged from the mouth.

From the preceding it is seen that liquids may be discharged from various parts of the body of insects and that this phenomenon is not restricted solely to beetles.

Leydig (1859) was the first to make sections through the femoro-tibial articulations of *Timarcha*, *Coccinella* and *Meloe*. He thinks that the discharged liquid is blood for the following reasons: (1) No gland cells nor glandular apparatus of any kind were recognized; (2) the discharged liquid and blood have the same color; and (3) the discharged liquid contains presumably blood cells. He admits that this view is not well founded because he could not find any openings in the articular membrane through which the blood could pass.

Cuenot (1890) says that the discharged liquid from the legs of the meloid beetles, *Cantharis*, *Meloe*, *Mylabris* and *Cerocoma*, is completely odorless, but it is slightly poisonous. He thinks that this liquid is blood, although he did not study sections passing through the articulations. The same author (1894) states that when one touches *Timarcha*, *Adimonia*, *Coccinella* or *Meloe*, the beetles at once feign death. They fold the legs and antennæ under their bodies, fall to the ground and for a longer or shorter time assume a perfectly inactive attitude destined to deceive their enemies. At the moment when the insects roll on the ground, drops of a slightly viscid liquid are ejected from the mouths of *Timarcha* and *Adimonia*, but from the femoro-tibial articulations of the coccinellids and meloids. This liquid is yellowish or reddish in color. The discharged liquid of *Coccinella* has a strong and very disagreeable odor, and that of *Timarcha* is odorless, but has a persistent and astringent taste. He proved by experiments that this liquid is for defense.

Cuenot (1896b) summarizes his investigations by saying that *Timarcha, Galeruca, Megalopus,* coccinellids and meloids among the Coleoptera, and *Eugaster* and *Ephippiger* among the Orthoptera possess the phenomenon of reflex bleeding. When disturbed they feign death and eject drops of blood from the mouth, femoro-tibial articulations and from the articulations of the first pair of wings. In all these species the blood comprises toxic, caustic or repulsive products. It is an important means of defense against lizards and batrachians.

Lutz (1895) asserts that in the Coccinellidæ, blood coming from the distal end of the femur issues through a slit on either side of the articular membrane which surrounds the chitinous rods (Selane) to which the extensors of the tibia are attached. The blood exudes by a forced contraction of the abdomen and by the flexors of the tibia, and it is a voluntary act. It is a means of defense because the blood is actually quite repulsive to insectivorous animals. In *Timarcha, Meloe,* etc., as in the coccinellids, the device of ejecting blood from the femoro-tibial articulations is to permit the blood to escape from the legs rather than through the mouth.

Packard (1895) states that many beetles, such as the oil beetles *Meloe, Cantharis* and *Lytta,* emit drops of blood from the femoro-tibial articulations as a means of defense. The cantharadine produced by these insects is formed in the blood and in the genital organs. It is so extremely caustic that scavenger insects feeding upon the dead bodies of these beetles leave untouched the parts containing cantharadine. Coccinellids are also protected by a yellow mucilaginous and disagreeable fluid which is emitted from the sides of the thorax.

Of those who advocate the view that the discharged liquid is blood, Leydig is the only one who has studied sections passing through the femoro-tibial articulations. And even he admits that his view is not well founded, because he failed to find any openings at these articulations. Lutz has certainly mistaken some other structure for slits. Perhaps he has seen the olfactory pores which often lie where his supposed slits were observed.

The following authors believe that the discharged liquid is a glandular secretion.

Magretti (1881) imagines that the discharged liquid from *Meloe* is secreted by gland cells in the legs.

Beauregard (1885) saw a layer of large hypodermal cells beneath the chitin in sections through the articulations of the legs of *Meloe*. He imagines that these large cells are gland cells.

De Bono (1889) believes that the discharged liquid from *Timarcha* is a glandular secretion.

Porta (1903) says that the discharge of the secretion from *Coccinella*, *Timarcha* and *Meloe* is caused by a reflex phenomenon brought about by any excitement. The liquid is secreted by a glandular follicle in the reticulum formed from the fibers of connective tissue, situated in the wall of the middle intestine. The liquid has an acrid reaction, and it is perhaps only a bile secretion. He gives three reasons why this liquid is not blood: (1) It is inadmissible that insects should constantly pass such an important fluid; (2) after a prolonged excitation the liquid ceases to exude; and (3) it has an acrid reaction while we know that blood in all animals has an alkaline reaction. He fails to explain how this secretion reaches the exterior from where it is produced.

Berlese (1909) seems to think that the discharged liquid from *Meloe* is a mixture of blood and a secretion from hypodermal glands. In a diagram showing the anatomy of the leg at the femoro-tibial articulation, he figures a receptacle for containing the blood and shows how the blood is ejected through an aperture at this place in the leg. He also shows unicellular glands lying just beneath the hypodermis on both sides of the articulation. Each gland cell is almost spherical, has a conspicuous nucleus and a central vesicle, the ampulla, from which runs the efferent tube through the hypodermis and chitin to the exterior. · These gland cells are like the ones without reservoirs described by the present writer.

Of those who believe that the discharged liquid is a glandular secretion, only Beauregard and Berlese have studied sections passing through the femoro-tibial articulations. Berlese is the only one who has actually found gland cells at this place in the legs. His receptacle for containing the blood is perhaps the same as the special chamber described by the present writer. Since Leydig did not see an aperture in the articular membranes of *Timarcha*, *Coccinella* and *Meloe*, and as the articular membrane of *Epilachna* does not contain any aperture, it would seem that the aperture described by Berlese was only an artificial

opening in the chitin made when the material was sectioned. The present writer has examined the femoro-tibial articulations of the meloid beetles, *Cysteodemus armatus* and *Epicauta pennsylvanica*. The specimens were first treated with caustic potash and then the chitinous integuments were bleached with chlorine gas. No apertures were seen in or near the articular membranes, but innumerable, almost transparent, minute tubes were observed in and around the articular membranes. Minute gland pores were also seen widely distributed over the entire integument as described for *Epilachna*.

A survey of the literature pertaining to hypodermal glands shows that these glands vary much in structure.

As far as ascertained by the writer, Hoffbauer (1892) is the only one who has described hypodermal glands having reservoirs in the chitin. These are found in the elytra of *Tetropium* and *Halyzia*. The reservoir belonging to the gland in the former species is nothing more than a much expanded efferent canal through which the secretion passes to the exterior. The reservoir in the latter species is similar to that in *Epilachna*, except its efferent tube is a wide canal. In *Halyzia* the elongated cells stand vertically to the chitin with their narrower ends uniting with the mouths of the reservoirs. These gland cells have no ampullæ nor conducting tubes.

Tower (1903) found simple and compound hypodermal glands widely distributed in the elytra of *Leptinotarsa*, *Prionus* and *Orthosoma*, but they do not have ampullæ, conducting tubes nor chitinous reservoirs. These gland cells stand more or less vertically to the chitin with their extremely attenuated peripheral ends in contact with the mouths of minute pores.

Casper (1913) found hypodermal glands widely distributed over the entire body surface and appendages of *Dytiscus marginalis*. In structure they are similar to the ones without reservoirs described in this paper.

Lehr (1914) found hypodermal glands widely distributed in the elytra and wings of *Dytiscus marginalis*. In structure they are similar to those without reservoirs described by the present writer, except they are much larger.

SUMMARY.

Hypodermal gland pores are widely distributed over the entire integument of *Epilachna borealis*. Usually one, but sometimes two pores, lie near the base of almost every hair. Besides lying near the bases of the hairs, the pores on the tarsi and around the femoro-tibial articulations lie in groups. Two groups are located at the extreme proximal end of the tibia and two at the distal end of the femur around the articular membrane. All four groups contain 100 pores as an average. The articular membrane contains about 400 pores of another type.

These beetles always appear wet, and the more they are irritated the wetter they become. The wet appearance is caused by a hypodermal glandular secretion passing to the exterior through the pores. When irritated the beetles eject small drops of the amber-colored secretion from the femoro-tibial articulations through the four groups of pores near the articular membrane and those in the membrane. The discharge of the secretion is accomplished by putting the gland cells under a high blood pressure. This is made possible by a muscular contraction in the femur whereby the blood is forced into a specially devised chamber containing the gland cells which belong to the pores in and near the femoro-tibial articulation.

The gland cells are of two types. Those with reservoirs are several times larger than those without reservoirs. The former are widely distributed throughout the entire insect, while the latter is found only under the articular membrane of the femoro-tibial articulation. In other respects the two types are alike. Each gland cell has an ampulla and a conducting tube which either runs from the ampulla to the reservoir in the chitin or from the ampulla to the surface of the articular membrane. An efferent tube leads from the reservoir to the surface of the chitin.

The glandular secretion is bitter and has an offensive odor. Its chief purpose is that of protection, but it probably also aids the beetles in recognizing the different individuals and sexes of the same species.
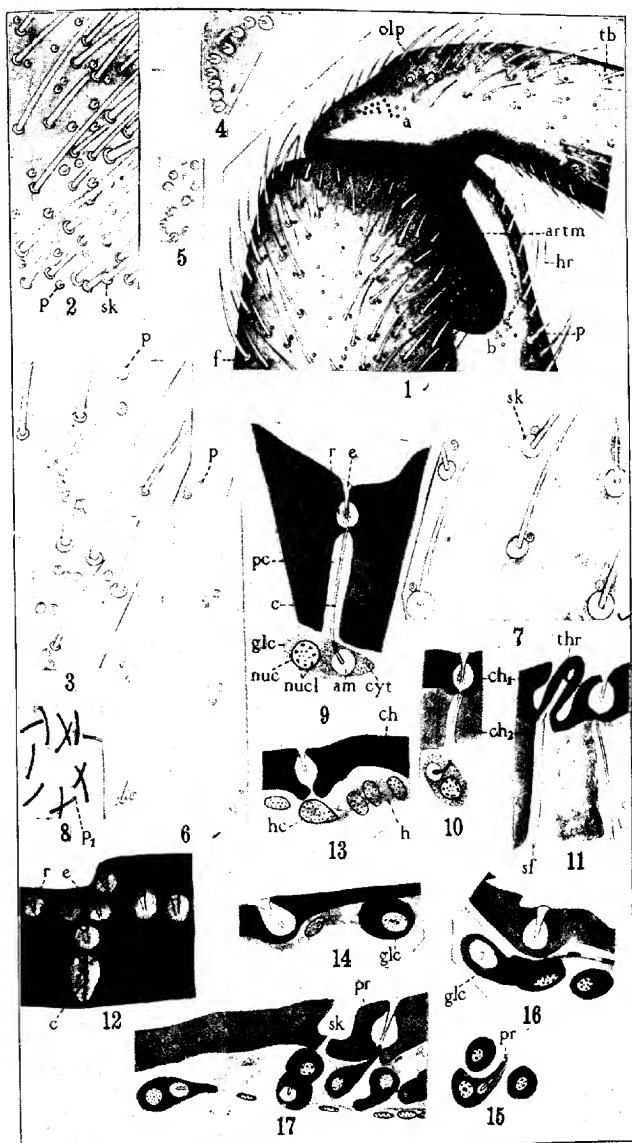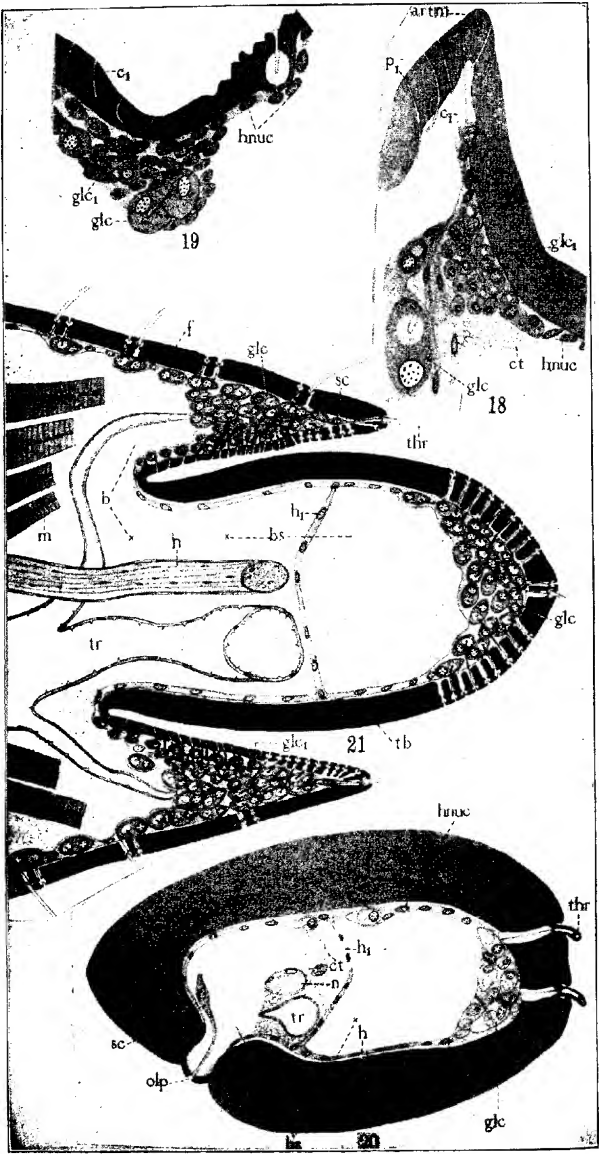
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EXPLANATION OF PLATES X AND XI.

All figures except diagram 21 are from camera lucida drawings made at the base of the microscope. The figures are enlarged as follows: 1, × 78; 2 to 7, × 280; 8 to 19, × 875; 20, × 350.

ABBREVIATIONS.

a—group *a* of pores on proximal end of tibia.
am—ampulla.
artm—articular membrane.
b—group *b* of pores on distal end of femur.
bs—blood sinus.
c—conducting tube of gland with reservoir.
c_1—conducting tube of gland without reservoir.
ch—chitin of beetle recently emerged.
ch_1—chitin formed before beetle emerges.
ch_2—chitin formed after beetle emerges.
ct—connective tissue.
cyt—cytoplasm.
e—efferent tube.
f—femur.
glc—gland cell with reservoir.
glc_1—gland cell without reservoir.
h—hypodermis.
h_1—membrane dividing lumen of leg into two chambers.
hc—hypodermal cell.
hnuc—hypodermal nucleus.
hr—hair.
m—muscle fiber.
n—nerve.
nuc—nucleus of gland cell.
nucl—nucleoli of gland cell.
olp—olfactory pore.
p—pore with reservoir.
p_1—pore without reservoir.
pc—pore canal.
pr—process of young gland cell.
r—reservoir.
sc—sense cell.
sf—sense fiber.
sk—socket of hair.
tb—tibia.
thr—tactile hair.
tr—trachea.

Figures 1 to 8 inclusive are superficial views of external ends of hypodermal gland pores of *Epilachna borealis*.

PLATE X.

Fig. 1. Femoro-tibial articulation of hind leg, showing groups *a* and *b* of hypodermal gland pores, 3 olfactory pores (*olp*), a hypodermal gland pore (*p*) at base of each hair, and articular membrane (*artm*) containing hypodermal gland pores (represented by white dots).

Fig. 2. Hairs and pores on first tarsal joint. Oblique view.

Fig. 3. Hairs and pores on fourth tarsal joint.

Fig. 4. Nine pores from group *b* on femur. Oblique view.

Fig. 5. Nine pores from group *a* on tibia. Slightly oblique view.

Fig. 6. Hairs and pores from tergum of prothorax.

Fig. 7. Hairs and pores from elytron, near base.

Fig. 8. Chitinous tubes connected with pores, seen by looking through articular chitin.

Figs. 9 to 12 inclusive are cross sections, showing structure of hypodermal glands having reservoirs in old *Epilachna borealis*.

Figs. 9 and 10. Complete hypodermal gland cells, showing the nucleus (*nuc*), nucleoli (*nucl*), cytoplasm (*cyt*), ampulla (*am*), conducting tube (*c*), pore canal (*pc*), reservoir (*r*), and efferent tube (*e*). Fig. 9 is from thick portion of outer margin of elytron, and Fig. 10 is from proximal end of tibia.

Fig. 11. Gland pore and tactile hair (*thr*) pore from distal end of femur.

Fig. 12. Oblique superficial section through tibia, treated with caustic potash 4 hours, showing that efferent tubes (*e*) and conducting tubes (*c*) are chitinous.

Figs. 13 to 17 inclusive are cross sections, showing origin of gland cells and conducting tubes of type having reservoirs in recently emerged beetles.

Fig. 13. Four hypodermal cells, one of which (*hc*) is about ready to change into a gland cell.

Fig. 14. Two hypodermal cells, one of which (*glc*) is now enlarged into a gland cell.

Fig. 15. Three young gland cells, one of which is sending out a process (*pr*) to form conducting tube. Figs. 14 to 16 are from a beetle emerged 1 hour.

Fig. 16. Three young gland cells from thick portion of elytron. One of these (*glc*) seems fully developed.

Fig. 17. Young gland cells from proximal end of tibia sending out processes (*pr*) to form conducting tubes. Figs. 17 and 18 are from beetles emerged 24 hours.

Figs. 18 and 19 are cross sections through articular membranes, showing type of glands without reservoirs.

Fig. 18. Conducting tubes (c_1) and gland cells (glc_1) without reservoirs, and 2 gland cells (*glc*) belonging to type having reservoirs from an old beetle.

Fig. 19. Origin of gland cells (glc_1) without reservoirs from hypodermal cells (*hnuc*). Also conducting tubes (c_1) and 2 gland cells (*glc*) with reservoirs from beetle emerged 1 hour.

Fig. 20. Cross section through extreme proximal end of tibia of hind leg, showing anatomy of leg, including tactile hairs (*thr*), olfactory pore (*olp*), gland cells (*glc*), membrane (h_1) dividing lumen of leg into two chambers, blood sinuses (*bs*), etc. The section is 5 microns thick and is from a beetle that had been kept in the laboratory all summer.

Fig. 21. Diagram of a section through femoro-tibial articulation, showing anatomy of leg at this place, including gland cells (*glc*) belonging to the two groups of pores on tibia (*tb*), gland cells belonging to the two groups on femur (*f*), and gland cells (glc_1) without reservoirs, etc. The femur (*f*) is cut longitudinally, but the tibia (*tb*) is cut across obliquely.

HOW GASES ENTER INSECTS.

WILLIAM MOORE,

Division of Economic Zoology, Minnesota Experiment Station,
St. Paul, Minnesota.

INTRODUCTION.

Few experiments have been performed to show how insects take in various gases, whether the gas enters through the spiracles alone, through other openings in the chitin, or even through the chitin. Schafer* has performed a few experiments in which he placed insects in the gas hydrogen sulphide until nearly dead, when they were removed and a warm solution of lead acetate was injected into their bodies by means of a fine hypodermic needle. A black precipitate of lead sulphide showed where the gas had penetrated. In these experiments only larger insects such as white grubs could be successfully used.

Chitin as a rule is rather an impermeable substance and the results in the larger insects showed that the gas had entered through the spiracles. The question arises, Do the smaller insects such as mealy bugs, white fly, soft scales, etc., which have a much thinner layer of chitin depend alone upon their spiracles for the penetration of gases into their bodies? After trying several different agents, it was found that osmic acid vapor could be used as a gas on the insects and would darken the tissues where it entered the insect.

METHOD.

The insect to be studied was placed in a small vial in its natural position on the leaf or stem and the vial suspended in a large bottle containing crystals of osmic acid. The bottle was then stoppered and placed under a bell-jar to prevent a leakage of the gas into the room. The insects remained in the gas for various periods of time, depending upon the insects, after which they were removed, placed in alcohol, and through xylene, finally being mounted in balsam for study.

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*Michigan Agricultural Experiment Station, Technical Bulletin, No. 11, July, 1911, pp. 16.

RESULTS.

White grubs or the larvæ of wood-borers, showed a blackened area about the spiracles only. Too long an exposure to the vapor causes a uniform blackening of the chitin. Mealy bugs exposed for two to four hours showed a black area around each spiracle, and in addition a black area around the anus, extending up the alimentary canal. The anal lobes which contain many wax glands were also blackened, showing that the gas had entered the wax pores. The wax of the mealy bug was not blackened by the treatment. This is of particular interest, as the mealy bug contains only two pairs of spiracles located near the anterior end of the body. Contrasted with the mealy bug, one finds that the immature stages of the white fly, which is well-protected by a wax coat, only shows a penetration of the gas through the spiracles. The white fly has four pairs of spiracles evenly distributed, one pair being located near the anus.

Spraying plants infested with mealy bugs with a weak soap solution to remove the wax greatly increases the ease with which these insects can be killed by hydrocyanic gas fumigation, while little effect is noticed in its efficiency for white fly.

A species of soft scale, Coccus sp., showed penetration through the spiracles, the anus and also the wax glands scattered about the body. Aphids show the spiracles marked, while some osmic acid seems to enter at the nectaries.

CONCLUSION.

These few experiments show that gases can penetrate through other parts of the body than the spiracles. It seems, however, that very thin chitin is impermeable to osmic acid. Even the vapor of osmic acid, however, is not a good penetrating agent. Oxygen and probably other gases, particularly hydrocyanic acid, which is extremely soluble in water has greater penetration and may even penetrate through thin layers of chitin.
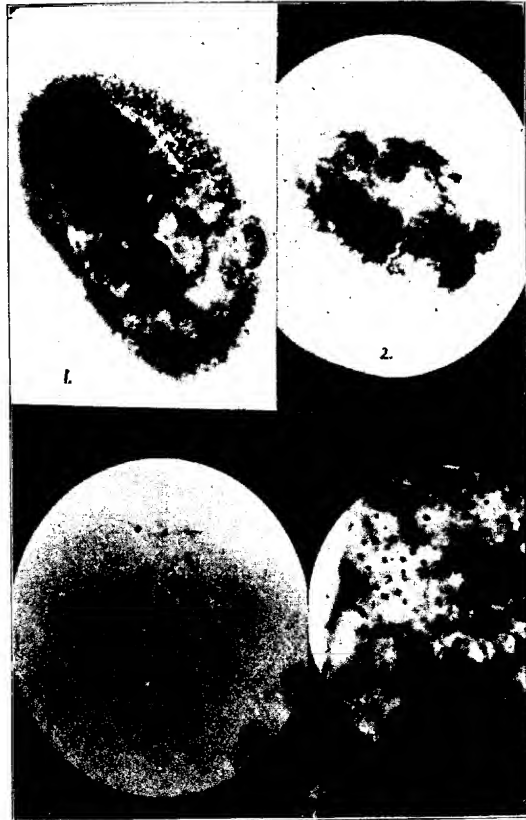
William Moore

EXPLANATION OF PLATE X.

1. Photomicrograph of soft scale, *Coccus* sp., after treatment with osmic acid.
2. Photomicrograph of mealy bug after treatment with osmic acid.
3. Photomicrograph of the anterior portion of immature white fly, showing penetration of osmic acid through the spiracles and along the trachea.
4. A portion of the soft scale, showing wax glands with dots caused by osmic acid.